TROPHIC DYNAMICS OF BOREAL LAKES IN A CHANGING NORTHERN LANDSCAPE

– IMPACTS OF LAKE DRYING AND FOREST FIRES

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TROPHIC DYNAMICS OF BOREAL LAKES IN A CHANGING NORTHERN LANDSCAPE – IMPACTS OF LAKE DRYING AND FOREST FIRES

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Abstract

The abundant lakes of northern latitudes are the primary breeding grounds for many waterbird species. In recent decades, temperatures in the north have increased by twice the global average. This substantial warming has caused lake drying and increased wildfires, both of which may impact waterbird habitats. Fires release nutrients locked in terrestrial resources, making them available for transport to lakes, while lake drying concentrates nutrients and other solutes into smaller water volumes. Increased nutrients may fundamentally alter ecosystem processes of lakes by changing the timing and abundance of phytoplankton blooms, which in turn affects the abundance of aquatic invertebrates – the primary food source for breeding waterbirds and their broods. I examined effects of forest fires and lake drying on ecosystems of Subarctic boreal lakes in the Yukon Flats, Alaska, documenting changes to (1) aquatic nutrient and chlorophyll concentrations, (2) aquatic invertebrate densities, and (3) abundance and occupancy of waterbirds. Nutrient, chlorophyll, and invertebrate levels were largely unaffected by a recent forest fire. This ecosystem stability transferred upward to waterbirds, as brood abundance was also unaffected by the fire. On drying lakes, nitrogen and phosphorus concentrations increased >200% and >100%, respectively, from the 1980s to present. At the same time, concentrations of 4 major ions increased, including increases of >500% for chloride and >100% for sodium. Nonetheless, chlorophyll levels, aquatic invertebrate abundance, and occupancy of waterbird broods were largely unaffected by these chemical changes on drying lakes. Overall, ecosystems of Yukon Flats were largely resilient to short-term effects of forest fires and rising chemical concentrations associated with lake drying. Moreover, this resilience spanned multiple trophic levels, from phytoplankton to aquatic invertebrates to waterbirds.

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Chapter 1

General Introduction

The highest global concentration of lakes occurs at Arctic and Subarctic latitudes, accounting for nearly half of the planet's surface freshwater (Schindler and Lee 2010, Verpoorter et al. 2014). These lakes provide important habitat for the region's wildlife, including migratory waterbirds that breed there in the tens of millions. In recent decades, Arctic and Subarctic latitudes have experienced a period of unprecedented warming, with temperatures having increased by at least twice the global average warming (Callaghan et al. 2004, New et al. 2011). These substantial temperature increases are likely to have both direct and indirect impacts on the structure and function of northern lake ecosystems, with potentially significant consequences for aquatic biota (Wrona et al. 2006).

Foremost, rising temperatures at high latitudes have been linked to long-term shifts in lake water balance, including net losses in lake surface area for Arctic and Subarctic regions of Alaska (Riordan et al. 2006, Rover et al. 2012), Canada (Smol and Douglas 2007, Carroll et al. 2011), and Siberia (Smith et al. 2005). Two of the primary processes likely responsible for reductions in surface area of northern lakes are: (1) increased evaporation, whereby warmer air and water temperatures and a longer ice-free season increase evaporative water losses, and (2) accelerated permafrost degradation, in which newly-thawed soils enhance sublacustrine drainage of lake waters. Importantly, both of these processes, in addition to causing lake drawdowns, may also cause substantial changes to water chemistry, including eutrophication and salinization. Increased evaporation, if not balanced by concurrent increases to water inputs, concentrates nutrients and ions into smaller water volumes (Smol and Douglas 2007). At the same time, thawing permafrost exposes previously frozen organic matter to decomposition and

mineralization, releasing nutrients and other solutes that may be flushed from soils to lakes (Petrone et al. 2006, Wrona et al. 2006).

In addition to losses in lake surface area, warming climates at northern latitudes have caused increased fire activity, especially in the vast boreal forest biome (Kelly et al. 2013). Fires are one of the major natural disturbances in the boreal forest, and the area burned in the North American boreal forest tripled from the 1960s to 1990s (Kasischke and Turetsky 2006). During the 1990s and 2000s alone, >25% of Alaska's boreal forest burned (Kasischke et al. 2010). Fires release nutrients and organic matter locked in terrestrial boreal resources such as soils and vegetation, making them available for transport to lake ecosystems. For example, a boreal forest fire in Subarctic Canada caused 1.5- and 2-fold increases in lake concentrations of total nitrogen and total phosphorus, respectively (Scrimgeour et al. 2001). Moreover, because much of the boreal forest is underlain by permafrost, particularly at Subarctic latitudes, fires may have an especially pronounced impact on lake water chemistry. Fires accelerate permafrost degradation by removing vegetative layers and organic material that insulate the ground (O'Donnell et al. 2011), thereby releasing previously frozen nutrients and ions that may be flushed to nearby lakes.

For lakes of northern regions, increased concentrations of nutrients and ions, whether from losses in surface area or forest fires, may significantly impact the structure and function of their ecosystems. In general, nitrogen and phosphorus, rather than light or carbon, most typically limit productivity in shallow Arctic and Subarctic lakes (Ogbebo et al. 2009). Accordingly, as nitrogen and phosphorus concentrations increase, lakes may experience elevated productivity, whereby the added nutrients stimulate primary production and thereby add more overall energy to the lake ecosystem (Waide et al. 1999, Dodson et al. 2000). Increased primary productivity may drive increases in secondary production of aquatic herbivores, which are typically

dominated by aquatic invertebrates in shallow northern lakes (Peterson et al. 1993, McEachern et al. 2000, Slavik et al. 2004). In turn, top predators may benefit from more abundant aquatic invertebrates, including breeding waterbirds and their chicks (Kelly et al. 2006, Lewis et al. 2015). In this manner, increased nutrient concentrations may ultimately cascade across multiple trophic levels, from primary producers to invertebrate consumers to top predators (Carpenter et al. 1985). Finally, in addition to nutrients, elevated ion concentrations on northern lakes may also impact lacustrine biota by raising baseline salinity levels. In particular, organisms with low salt tolerances, including certain species of aquatic invertebrates, may become osmotically stressed, causing reduced growth or death (James et al. 2003).

In Chapter 2 of this dissertation I addressed factors driving distributions and diversity of waterbird broods on Subarctic lakes in the Yukon Flats, Alaska. Lakes of the Yukon Flats are internationally important breeding habitats for waterbirds, annually supporting approximately 1.6 million individuals from nearly 30 species. During the summer, waterbirds are the top predators on these lakes, feeding primarily on aquatic invertebrates (Lewis et al. 2015). We used an occupancy modeling framework to assess the relative roles of invertebrate abundance, water chemistry, and habitat structure in determining distributions and species richness of waterbird broods on lakes of the Yukon Flats. In doing so, I provide a baseline understanding of how potential changes to lake ecosystems, including changes to shrinking and fire-impacted lakes, may ultimately impact waterbird populations.

In Chapter 3, I describe changes to water chemistry on shrinking lakes of the Yukon Flats and assess potential mechanisms behind such changes. From 1979 to 2009, 9–16% of Yukon Flats lakes decreased in surface area extent (Rover et al., 2012), with unknown effects on aquatic ecosystems. I compared water chemistry samples collected from 1985–1989 to those collected

between 2010–2012 for a suite of shrinking, stable, and expanding lakes in the Yukon Flats. I described differences between the two time periods in chemical concentration of two aquatic nutrients of high biologic importance (total nitrogen, total phosphorus) and four major ions (calcium, chloride, magnesium, sodium). To provide insight into possible mechanisms behind changes in water chemistry, I examined patterns of nutrient and ion concentrations in relation to lake-specific variation in amount of evaporation and permafrost cover.

Chapter 4 assesses the impacts of chemical changes in shrinking lakes on lacustrine biota. I predicted that rising nutrient concentrations observed in shrinking lakes would trophically propagate through lake ecosystems, affecting biota from primary producers through top predators. Moreover, higher ion concentrations may exceed physiologic thresholds of aquatic organisms with low salt tolerance. I examined ecosystem changes across 3 broad trophic levels in shrinking versus stable lakes of the Yukon Flats from 1985–1989 to 2010–2012, in which chemical changes over this same time period were largely limited to shrinking lakes. Specifically, I examined decadal changes to abundance and distributions of organisms from 3 successive trophic levels: phytoplankton, aquatic invertebrates, and waterbirds.

Chapter 5 of this dissertation examines the short-term impacts of a large forest fire on lake ecosystems. The Yukon Flats is one of the most flammable boreal regions in North America, yet continues to experience increased fire activity (Kelly et al. 2013). Charcoal records from lake cores indicate that fire frequency in the Yukon Flats from the most recent decades far surpasses that of the past 10,000 years (Kelly et al. 2013). Taking advantage of a natural forest fire at one of our study sites, I examined short-term impacts of fires on water chemistry, phytoplankton, aquatic invertebrates, and waterbirds. Moreover, I was able to employ a before-after-control-impact study design, with pre- and post-fire data from both burned and unburned

lakes; such strong study designs are rarely available for naturally occurring fire events such as ours.

In summary, the various chapters of my dissertation, though covering distinct topics, are each connected by a common research question: how will ecosystems of northern lakes respond to climate change? In the chapters that follow, I provide novel insight into this important and timely question.

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Chapter 2

Species richness and distributions of boreal waterbird broods in relation to nesting and brood-rearing habitats[1]

2.1 Abstract

Identification of ecological factors that drive animal distributions allows us to understand why distributions vary temporally and spatially, and to develop models to predict future changes to populations – vital tools for effective wildlife management and conservation. For waterbird broods in the boreal forest, distributions are likely driven by factors affecting quality of nesting and brood-rearing habitats, and the influence of these factors may extend beyond singles species, affecting the entire waterbird community. We used occupancy models to assess factors influencing species richness of waterbird broods on 72 boreal lakes, along with brood distributions of 3 species of conservation concern: lesser scaup (*Aythya affinis*), white-winged scoters (*Melanitta fusca*), and horned grebe (*Podiceps auritus*). Factors examined included abundance of invertebrate foods (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), physical lake attributes (lake area, emergent vegetation), water chemistry (nitrogen, phosphorus, chlorophyll *a* concentrations), and nesting habitats (water edge, non-forest cover). Of the 5 invertebrates, only amphipod density was related to richness and occupancy, consistently having a large and positive relationship. Despite this importance to waterbirds, amphipods were the most patchily distributed invertebrate, with 17% of the study lakes containing 70% of collected amphipods. Lake area was the only other covariate that strongly and positively influenced

[1]Lewis, T.L., M.S. Lindberg, J.A. Schmutz, M.R. Bertram, and A.J. Dubour. 2014. Species richness and distributions of boreal waterbird broods in relation to nesting and brood-rearing habitats. Journal of Wildlife Management 79:296–310.

species richness and occupancy of scaup, scoters, and grebes. All 3 water chemistry covariates, which provided alternative measures of lake productivity, were positively related to species richness but had little effect on scaup, scoter, and grebe occupancy. Conversely, emergent vegetation was negatively related to richness, reflecting avoidance of overgrown lakes by broods. Finally, nesting habitats had no influence on richness and occupancy, indicating that, at a broad spatial scale, brood distributions were largely driven by the presence of quality brood-rearing lakes, not nesting habitats. Our findings are relevant to generating conservation plans or management goals; specifically, boreal lakes with abundant amphipods and surface areas >25 ha are important habitat for waterbird broods and merit conservation, especially given the patchy distribution of amphipods. Moreover, these high quality brood-rearing lakes are much rarer, and thus more constraining, than are quality nesting habitats, which are likely abundant in the boreal forest.

2.2 Introduction

Fundamentally, animal distributions are determined by a combination of ecological factors required for survival and reproduction, and hence on the spatial and temporal patterns of variation in these factors (Brown 1984, Scott et al. 2002). Identification of such factors, particularly those that have a mechanistic role, allows us to interpret why distributions vary in the ways they do, and to develop accurate predictions of future changes to populations – vital tools for effective wildlife management and conservation (Wiens and Rotenberry 1981, MacKenzie et al. 2006). For many species, ecological factors driving distributions are both numerous and diverse, commonly including such variables as food availability, climate, habitat structure, and predator refugia. Additionally, these factors may occur at a multitude of scales,

from the habitat patch to the landscape (Orians and Wittenberger 1991, Sunarto et al. 2012), and may change in accordance with seasonal shifts in the life cycle (Paasivaara and Poysa 2008). Given the complexity of factors and scales involved, studies assessing determinants of animal distributions should simultaneously consider a variety of ecological factors across multiple spatial and temporal scales (Morrison et al. 2006). Moreover, the management and conservation value of such studies can be maximized by identifying those factors that affect multiple species, rather than single species of interest.

Brood distributions of obligate waterbirds such as ducks and grebes are driven by a variety of ecological factors, many of which are specific to the demands of developing chicks. In particular, broods require highly productive aquatic habitats that provide abundant food, ensuring rapid growth and fledging during the short summer season (Sjoberg et al. 2000). In boreal lakes, nitrogen and phosphorus, rather than light or carbon, most typically limit productivity (Ogbebo et al. 2009). As such, broods may prefer lakes with higher concentrations of phosphorus and nitrogen because the higher primary productivity on these lakes radiates through the food web to upper-level consumers such as waterbirds (Stacier et al. 1994, Sjoberg et al. 2000). Diets of waterbird chicks consist mainly of aquatic invertebrates and their growth and survival is positively correlated with invertebrate abundance (Cox et al. 1998, Sjoberg et al. 2000). Although an invertebrate diet allows for rapid growth, the attainment of flight requires an extended period of feather growth, making flightless chicks susceptible to predation. Accordingly, boreal lakes must also provide cover from predators, typically in the form of emergent vegetation (Bloom et al. 2012, Walker et al. 2013).

The ecological factors discussed above primarily affect brood distributions and habitat selection at the scale of the brood-rearing lake; however, the boreal breeding season consists of

both nesting and brood-rearing, and nesting distributions are driven by their own unique set of ecological factors. Successful nesting requires semi-terrestrial habitats with high vegetative concealment (Pasitschniak-Arts and Messier 1995), whereas brood-rearing requires productive aquatic habitats (Stacier et al. 1994, Sjoberg et al. 2000). Nonetheless, both habitats must simultaneously occur in close proximity because, upon hatching, relatively immobile ducklings leave the nest for brood-rearing lakes (Paasivaara and Poysa 2008). Thus, the brood-rearing lake can be thought of as a habitat patch embedded in a terrestrial matrix of potential nesting habitat. Based on this life history, we would expect spatial distributions of waterbird chicks to depend on both patch (i.e., brood-rearing lakes) and landscape characteristics (i.e., matrix of terrestrial nesting habitat).

We used an occupancy modeling framework to assess relative roles of invertebrate abundance, aquatic productivity, and habitat structure in determining distributions and species richness of waterbird broods on boreal lakes, while also accounting for the different spatial scales of breeding (nesting landscape vs. brood-rearing lake). Because of recent conservation concern and their strong reliance on aquatic invertebrates, we conducted discrete single species occupancy models for broods of lesser scaup (*Aythya affinis*; hereafter scaup), white-winged scoters (*Melanitta fusca*; hereafter scoters), and horned grebes (*Podiceps auritus*; hereafter grebes). To assess the complete waterbird community, we used multi-species occupancy models to estimate species richness, which included broods of both diving and dabbling species. Occupancy models account for imperfect detection and are thus appropriate for our data because the small size and secretive nature of waterbird chicks typically leads to low probabilities of detection which, if unaccounted for, yield biased estimates of occupancy and species richness (Walker et al. 2013). Under this framework, we tested 4 non-exclusive hypotheses: 1) Emergent

vegetation will be positively related to brood occupancy and richness because it provides necessary cover from predators. 2) Because brood-rearing lakes must be closely located to appropriate nesting habitats, brood richness and occupancy of lakes will be influenced by both habitat types. 3) More productive lakes, defined by their relatively high concentrations of nitrogen, phosphorus and chlorophyll *a*, will have greater species richness and probabilities of brood occupancy. 4) Because of the high food demands of rapidly growing waterbird chicks, aquatic invertebrate abundance will be an important predictor of brood occupancy and richness. Finally, to ascertain which type of aquatic invertebrates to target for management purposes, we explored the relative influence of the 5 most common aquatic invertebrate groups on brood richness and occupancy.

2.3 Study Area

We conducted our research in the Yukon Flats, a 25,900 km^2 boreal basin in interior Alaska bisected by the Yukon River and encompassed by the Yukon Flats National Wildlife Refuge. The region contains more than 40,000 lakes and wetlands and is largely pristine habitat, with no appreciable road infrastructure and approximately 1,200 permanent inhabitants. Mixed boreal forest covers much of the area and is dominated by black (*Picea mariana*) and white spruce (*P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.). We conducted our research on 6 randomly selected study plots spread across the Yukon Flats (Fig. 1). These plots measured 10.36 km^2 and contained 6–17 lakes, for a total of 72 study lakes. Lakes varied greatly in size from <1 ha to >200 ha (Table 1), but were uniformly shallow, rarely measuring deeper than 2 m. Most study lakes functioned largely as closed basins, with no well-defined surface inlets or

outlets. This combination of shallow depth and lack of surface outlets precluded fish populations in all our study lakes.

2.4 Methods

We sampled each study lake 1–2 times per month (Jun–Aug) in 2 of 3 years (2010–2012) for waterbirds, aquatic invertebrates, and water chemistry, with the exception of 17 lakes that we sampled in all 3 years. This sampling design achieved an overall balance in sample effort, whereby we sampled each lake a total of 4 times per summer in 2010 and 2011, and 3 times per summer in 2012. We began each lake visit by surveying for waterbirds, which included all species of waterfowl, grebes, and loons. We timed our surveys to cover the breeding cycle, from nesting (early Jun) through brood-rearing (late Jun–Aug). We recorded species, sex, and age (adult vs. chick) of each individual observed on the lake. Each of our waterbird surveys consisted of 2 independent counts conducted over a 1–2 day period, allowing us to estimate detection probability (see Statistical Analyses below; Royle 2004). For smaller lakes, in which we could survey the entire area from 1 viewing location, unique observers conducted repeat counts back-to-back. Larger lakes, however, required the observer to move among multiple survey points by canoe, and these movements potentially affected waterbird detection on subsequent counts. Thus, under the assumption that observer-effects decrease with time since survey, we separated repeat counts on large lakes by 24 hours to establish independence between counts.

We collected 8 liters of water from near each lake's center point and 25 cm below the surface to measure water chemistry. Our study lakes, because of their shallow depths, are frequently mixed and thermal stratification is ephemeral (Heglund and Jones 2003); thus, the lake's center point provided a representative location from which to gauge its general water

chemistry status. We used water samples to measure concentrations of total nitrogen, total phosphorus, and chlorophyll *a*. See Lewis et al. (2014) for a complete description of water chemistry sampling, including laboratory techniques.

We collected aquatic invertebrates along sampling transects located at random locations along lake perimeters and oriented perpendicular to shore. We scaled number of transects to lake area and each lake had a minimum of 2 and a maximum of 21 transects. Abundance and type of aquatic invertebrates are related to aquatic vegetation (Gregg and Rose 1985). Thus, along each transect, we collected 1 invertebrate sample per unique vegetative zone, and a typical transect contained 2–3 samples. Vegetative zones included both emergent and submergent vegetation, with the most common plants being cattail (*Typha latifolia*), pondweed (*Potamageton* spp.), sedge (*Carex* spp.), and hornwort (*Ceratophyllum demersum*). In the event that we encountered ≤1 vegetative zone, we collected an extra sample in the open water zone. We used a D-frame sweep net (0.5-mm mesh) to collect samples from the water column, pulling it horizontally for 1 m just below the water surface and through the vegetation. We identified invertebrates to the family level and converted counts to volumetric densities (individuals/m^3).

We quantified attributes of each lake and the surrounding terrestrial habitat at 2 distinct spatial scales: brood-rearing lake versus nesting landscape. We measured brood-rearing attributes at the scale of the lake and included lake area and amount of emergent vegetation. This scale reflects the limited mobility of broods in the Yukon Flats, which were generally confined to 1 lake during brood-rearing (Corcoran et al. 2007, Safine and Lindberg 2008). We obtained lake areas from the National Hydrography Dataset, United States Geological Survey. To quantify emergent vegetation, we hand-drew perimeters of emergent zones onto aerial photographs in the field during July 2012, then later digitized photos into a geographic information system. We

mapped emergent vegetation during July to coincide with its maximum spatial extent. To normalize each lake's emergent zone by its respective lake size, we divided area of emergent vegetation (m^2) by open water area (m^2) and used this ratio in all subsequent analyses.

We measured nesting attributes at a scale approximating the maximum distance that broods may move upon hatching. In the Yukon Flats, scaup and scoters were documented moving broods up to 1.5 km from nests to brood-rearing lakes (Corcoran et al. 2007, Safine and Lindberg 2008). Thus, we created a buffer of 1.5 km around each lake and quantified nesting attributes within this buffer. That is, the buffer represents the spatial zone around each lake in which its broods may have originated. We did not create buffers for grebes, nor quantify their nesting attributes, because they nest on lakes or lake shorelines and rear their broods on the same lake (Ulfvens 1988). Nesting attributes included water edge (total distance of edges in buffer) and non-forest cover (% of buffer not covered by forest). Water edge, which quantifies the tendency of waterbirds to nest near waterbodies, is a summary measure of all shorelines located within the 1.5-km buffer and was calculated from the National Hydrography Dataset. Non-forest cover quantifies nesting vegetation and was obtained from the 2001 National Land Cover Database (Homer et al. 2004). Scaup typically nest in herbaceous vegetation, avoiding thick forest cover (Corcoran et al. 2007), whereas scoters favor forested habitats, avoiding open areas (Safine and Lindberg 2008). Thus, if nesting habitat is a significant determinant of lake occupancy, we would expect that non-forest cover is positively related to brood occupancy for scaup and negatively related for scoters.

Focal Species Analysis

We used an occupancy-modeling framework to assess factors explaining distributions of scaup, scoter, and grebe broods on lakes of the boreal forest, while adjusting for detection probability. We converted counts of each species per lake per survey to presence (1) or non-presence (0); a species was considered present if ≥1 chick was detected. This created a double encounter history for each survey (e.g., 01: species undetected on first encounter, detected on second encounter). For each species, we excluded all survey data per year that occurred prior to that year's first chick sighting. We used single-season occupancy models (MacKenzie et al. 2006) to estimate 2 parameters: probability of occupancy of a lake by a brood (ψ), and probability that a brood was detected given presence (p). We used the R package unmarked to fit occupancy models using maximum likelihood estimation (Fiske and Chandler 2011). We used single-season models because our primary interest was how birds were distributed among lakes in relation to covariates, not how occupancy changed over time (MacKenzie 2005). Before fitting models, we explored correlations between our covariates (Table 2), finding that none were overly correlated (i.e., Pearson correlation coefficient > 0.60; Bausell and Li 2002), and normalized all continuous covariates, such that their mean value was 0.

For each waterbird species, we modeled p in relation to 2 covariates: observer, which classifies surveyors as experienced or inexperienced, and amount of emergent vegetation, which is used by broods for cover and thus affects detection. Estimation of p was not our primary interest and we had reason to believe that both variables were significant; thus we chose to include both variables in every model. To determine important covariates for describing ψ for each waterbird species, we sequentially tested biologically feasible combinations of covariates in 4 stages: 1) lake and landscape covariates – lake area, emergent vegetation, water edge, and non-

forest cover; 2) water chemistry – total nitrogen, total phosphorus, and chlorophyll *a* concentrations; 3) aquatic invertebrate density – Amphipoda, Diptera, Gastropoda, Hemiptera, and Odonata densities; 4) year – 2010, 2011, and 2012. The best-fitting model from each lower-order stage, as determined by corrected Akaike's Information Criterion (AIC_c), served as the model template for each subsequent stage (Amundson and Arnold 2011). At each stage, we considered all combinations of additive models, with the exception that the covariates from the lower-order template model were included in every model. Additionally, we included an intercept-only null model for comparison in stage 1. We used this stage-wise approach to model selection to restrict the number of models in our model set and the number of covariates in any single model, given the large number of additive model combinations (i.e., $2^{12} - 1$ models). Likewise, we did not use models with interaction terms to restrict the size of our model set. We considered models with 1 additional covariate competitive only if they resulted in AIC_c scores lower than the simpler model and do not report non-competitive models, with the exception of the simplest models at each stage (i.e., template model + 1 covariate). Reporting the simplest models at each stage, even if they are noncompetitive, is necessary to assess the degree to which each covariate affects the AIC_c value. Finally, for our water chemistry and invertebrate covariates that we sampled multiple times per year, we used only those values which most closely aligned temporally with each brood survey; for example, we paired brood surveys from July with invertebrate and water chemistry data from July.

Our model set for grebes differed slightly from that explained above because of their unique nesting ecology. Grebes nest on lakes, typically in emergent vegetation, and cannot move their broods overland, forcing them to use the same lake for both nesting and brood-rearing (Ulfvens 1988). Thus, in the first stage of model fitting, we removed the 2 covariates (non-forest

cover, water edge) describing nesting habitats in the landscape surrounding the lake. All other covariates used in our analysis of grebe occupancy are identical to those used for scaup and scoters.

We based our inference of covariates on model selection, as described above, AIC_c model weights (w_i), and precision of parameter estimates, which we estimated using model-averaging (Burnham and Anderson 2002). When 95% confidence intervals overlapped 0, we deemed the covariate uninformative. We used a logit link function to determine parameter estimates and standard errors, which are presented without back transformation.

Species Richness Analysis

For analysis of species richness, we used multi-species occupancy models (Dorazio and Royle 2005), which have been previously used to estimate total community richness while also accounting for detection heterogeneity (Zipkin et al. 2010). These hierarchical models estimate species-specific occupancy and detection parameters by assuming that each of the species parameters was drawn from a common (community-level) distribution (Zipkin et al. 2010). The benefit of this approach is that inference can be made for species with few detections that otherwise would be impossible to model on their own (Link and Sauer 1996, Tingley and Beissinger 2013). We modeled probability of occupancy using the same set of covariates as the focal species models. However, because these models were conducted in a Bayesian setting that did not easily permit model selection, we analyzed each stage individually, with the exception that year was no longer included as a stage. All of the covariates from each stage comprised a distinct model, for a total of 3 models: lake and landscape, water chemistry, and aquatic invertebrates. Further, we included lake area in all 3 models because of its presumed strong

relationship to species richness (Dodson et al. 2000). We analyzed each stage as an individual model to restrict the number of covariates in any single model given the high number (12) of overall covariates. Finally, we modeled probability of detection as a function of ordinal date in all 3 models to account for time-dependent changes in size and behavior of waterbird chicks, especially for the dabbler species, that may affect detection.

We performed Bayesian analysis of the models using R2WinBUGS in program R (Sturtz et al. 2005), which calls on program WinBUGS (Lunn et al. 2000) to run Markov chain Monte Carlo simulations. We used the model code provided by Zipkin et al. (2010), which was designed to estimate species richness in relation to habitat covariates via multi-species occupancy models. We did not augment our data with all-zero matrices for unobserved species because our primary interest was not estimation of total species richness of the region but rather relating survey-specific richness estimates to covariates; hypothetic species added via data augmentation lack independent survey-specific covariate relationships (Kery and Royle 2008, Tingley and Beissinger 2013). As well, we were confident we observed nearly the full species assemblage of waterbird broods in our study area based on 5 years of prior surveys on the same lakes (Heglund 1992). We used the same uninformative prior distributions as described by Zipkin et al. (2010) and assessed model convergence using the R-hat statistic (Gelman and Hill 2007). Drawing from the posterior distribution, models estimated a survey-specific occupancy probability for each waterbird species, from which the sum of these occupancy rates provided our measure of species richness. Hence, the occupancy models do not build in explicit relationships between species richness and covariates. Instead, we inferred these relationships from 1) visual inspection of plotted relationships between covariates and survey-specific mean posterior richness estimates, with attention to degree of variance associated with our richness

estimates (i.e., 95% credible intervals), and 2) simple regression models that described the shape of the relationship between survey-specific mean posterior richness estimates and each covariate (Tingley and Beissinger 2013). Specifically, with survey-specific richness serving as the response variable, we fit 4 regression models for each covariate: intercept-only, linear, quadratic, and log-transformed models. We used AIC_c to select the best-fitting model for each covariate. We removed extreme values for each covariate from the regression if we deemed them to have excessive influence. Finally, these regression models used a response variable, species richness, which we also estimated (Link et al. 2002). Accordingly, we augmented our AIC_c model selection exercise with 'expert opinion', in which we visually verified the model fit with respect to the 95% credible intervals associated with each species richness estimate.

2.5 Results

Focal Species Models

We conducted 583 duplicate waterbird surveys over 3 years, detecting scaup, scoter, and grebe chicks on 24%, 7%, and 25% of surveys, respectively. In stage 1 of our model selection, we investigated habitat characteristics across 2 spatial scales: brood-rearing lake versus nesting landscape. Lake occupancy of scaup (Table A1) and scoters (Table A2) was not influenced by nesting habitat, as all models including non-forest cover and water edge received no model support ($w_i = 0.0$). Conversely, attributes measured at the scale of the brood-rearing lake (lake area, emergent vegetation) were much stronger predictors of lake occupancy. Lake area was strongly and positively related to occupancy for all 3 waterbird species. Lakes >40 ha had probabilities of occupancy near 1.0 for scaup and grebes, whereas scoters preferred even larger lakes, nearing a probability of 1.0 on lakes >100 ha (Fig. 2). Models including emergent

vegetation cover were supported for grebes (Table A3), but not for scaup (w_i = 0) and scoters (w_i = 0). Occupancy of grebes was positively related to emergent vegetation (β = 0.40 ± 0.15 [SE]; Table 3), being greater on lakes with higher vegetative cover (Fig. 2).

In the second stage of model selection, we assessed effects of water chemistry on brood occupancy. We collected 535 water samples over 3 years, and total nitrogen and phosphorus concentrations were generally high across our study lakes, averaging 2,597 and 311 µg/l, respectively (Table 1). Models with total nitrogen and phosphorus were generally not well supported for all 3 waterbird species (Table A1). Total nitrogen was included in the top model for grebes (w_i = 0.46; Table A3) and total phosphorus in the top model for scoters (w_i = 0.63; Table A2); however, both parameters had confidence intervals that widely overlapped 0 (Table 3), indicating they had little influence on occupancy. Chlorophyll *a* concentration was included in the top-ranked model for grebes (w_i = 0.46), but was not well supported for scaup (w_i = 0.19) or scoters (w_i = 0.06). Probability of lake occupancy by grebes was negatively related to chlorophyll *a* (β = –0.73 ± 0.34; Table 3), approaching 0 on lakes with extremely high (>100 µg/l) chlorophyll levels (Fig. 2).

We examined the influence of aquatic invertebrate density on lake occupancy in our third stage of model selection. We collected 4635 invertebrate samples over 3 years, containing 345,774 individuals. Of the 5 common aquatic invertebrate orders in our lakes, mean Diptera densities were the highest, followed in descending order by Amphipoda, Gastropoda, Odonata, and Hemiptera (Table 1). Distribution of invertebrate densities across our study lakes was more skewed for amphipods than for the other invertebrate orders (Table 1); amphipods were absent altogether from the bottom quartile of study lakes, ordered by ascending density, whereas densities of the upper quartile exceeded 225/m^3. Amphipod density was the only invertebrate

covariate included in the top model for all 3 waterbird species, being strongly and positively related to probability of lake occupancy for each (Table 3). On lakes without amphipods, probability of occupancy was 0 for scoters and approximately 0.30 for scaup and grebes, whereas probabilities neared 1.0 for all 3 waterbird species at amphipod densities >4,000/m^3 (Fig. 2). Hemiptera density was also in the top model for scoters (w_i = 0.64; Table A2), though it was unsupported for scaup (w_i = 0.07; Table A1) and grebes (w_i = 0; Table A3); however, its confidence interval widely overlapped 0 (Table 3), suggesting it had little genuine influence on scoter occupancy. The remaining covariates of Diptera, Gastropoda, and Odonata were not well supported in model sets for all 3 waterbird species.

For the final stage of model selection, we examined variability in lake occupancy across the 3 years of our study. Year was supported for scaup, indicating that occupancy probability of scaup ducklings was lower in 2011 versus 2010 and 2012 (Table 3). For scoters (Table A2) and grebes (Table A3), however, year received little model selection support and had parameter estimates with confidence intervals that overlapped 0 (Table 3). Finally, for all 3 waterbird species, detection probability was not well explained by either of the 2 variables used in our model sets (observer, emergent vegetation cover). Detection probabilities, as determined from a null detection model, were 0.90 ± 0.02 for scaup, 0.91 ± 0.05 for scoters, and 0.86 ± 0.03 for grebes.

Species Richness Models

We observed 17 species of waterbird chicks, including 8 diving waterfowl, 6 dabbling waterfowl, 2 grebe, and 1 loon species (Table B1). The quadratic model provided the best fit with species richness for landscape covariates that described nesting habitats (water edge, non-

forest cover; Table 4). However, both covariates had shallow quadratic curves in relation to richness (Fig. 3), offering little explanatory power. Moreover, survey-specific richness estimates (i.e., the scatterplot in Fig. 3) had widely ranging 95% credible intervals across the range of values for both water edge and non-forest cover (Fig. 3). Conversely, covariates measured at the scale of the brood-rearing lake (lake area, emergent vegetation) were strongly related to species richness, being best described by a quadratic fit (Table 4). Richness increased steeply in relation to lake area, increasing from approximately 2 to 16 waterbird species over the range of lake areas (Fig. 3). For emergent vegetation, the quadratic fit with species richness decreased across the range of values, with richness generally being lowest on lakes with the most emergent vegetation (Fig. 3).

The log model, where the covariate was log-transformed, provided the best fit for each water chemistry covariate: total nitrogen, total phosphorus, and chlorophyll *a* concentration (Table 4). Further, the direction and magnitude of the log-linear relationship was quite similar for each covariate; species richness increased across the covariate range, from near 0 to 8–10 species at the highest concentrations (Fig. 3). Visual inspection of survey-specific richness estimates, however, revealed a fair amount of uncertainty in the magnitude of this relationship, especially at intermediate covariate values. Nonetheless, the relationship is clearly positive for all 3 water chemistry covariates, each of which provides an indirect measure of aquatic productivity. Visual inspection also suggests a stronger and more consistent relationship between species richness and total phosphorus; almost all survey-specific richness estimates at log total phosphorus values > 5 µg/l had 95% credible intervals that did not overlap 0 (Fig. 3).

The quadratic model was the best model for Amphipoda, Diptera, and Gastropoda, whereas the log model provided the best fit for Hemiptera and the linear model for Odonata

(Table 4). However, only Amphipoda density appeared to have a strong and positive relationship with richness. The quadratic relationship estimated a 5-fold increase in richness across the range of amphipod densities, from 2–3 to >15 waterbird species (Fig. 3). There also appeared to be a positive relationship between Gastropoda density and richness, although this relationship was much weaker with a high degree of variance and was driven by relatively few data points at higher Gastropoda densities (Fig. 3). Conversely, densities of Diptera, Hemiptera, and Odonata had no apparent relationship with species richness. All 3 invertebrate orders had relatively flat trend lines, in which richness varied little to none across their density ranges (Fig. 3).

2.6 Discussion

Of the 4 landscape covariates we investigated (lake area, emergent vegetation, water edge, non-forest cover), lake area was consistently the best supported, having a strong and positive relationship to species richness and occupancy of scaup, scoters, and grebes. The ecological importance of lake area, however, can be difficult to interpret under an occupancy framework because large lakes have more aquatic habitat and require more survey effort, thereby increasing the probability of detecting at least 1 brood. Although this sample design may have inflated the importance of lake area in our analyses, the unique habitat requirements of scaup, scoter, and grebe broods, along with our estimates of detection probability and chick abundance, collectively indicate that lake area had an important biological role in shaping brood occupancy patterns in the Yukon Flats. Firstly, scaup and scoter ducklings were unique among waterfowl broods in the Yukon Flats in that they generally retreated to open-water zones when disturbed, as opposed to hiding within emergent vegetation (T. L. Lewis, University of Alaska Fairbanks, personal observation) This is because both species are strong divers at early ages, often using their diving

ability to evade predators (Mikola et al. 1994). Moreover, similar to Kehoe (1989), we observed both species forming large crèches in open water areas when disturbed. Likewise, grebe chicks commonly dove when disturbed, although they used vegetative cover more frequently than did scaup and scoter broods (T. L. Lewis, University of Alaska Fairbanks, personal observation). Accordingly, scaup, scoter, and grebe chicks likely avoided smaller lakes in the Yukon Flats because the restricted, and often overgrown, open water zones limited their ability to use diving as an effective escape mechanism. Secondly, our high detection probabilities for these 3 species (scaup = 0.90, scoters = 0.91, grebes = 0.86) further highlighted their tendency to use the open water zones of larger lakes, which were the most highly visible zones during our surveys. Dabbling duck broods, in contrast, used vegetative concealment as their primary means of predator evasion, as reflected in their low detection probabilities (<0.50; Lewis 2015). Finally, our abundance estimates support our conclusion that lake area has an important biological role for broods; we observed a combined abundance of 72 scaup, scoter, and grebe chicks on lakes <1.0 ha (n = 22), versus 351 chicks on lakes of 1–10 ha (n = 33) and 3,165 chicks on lakes >10 ha (n = 17).

Our initial hypothesis was that richness and lake occupancy would be influenced by both nesting and brood-rearing lake habitats. However, variables that described nesting habitats had no effect on richness and lake occupancy, even though these variables spatially encompassed the complete nesting zone from which each lake's broods originated. Conversely, multiple variables measured at the brood-rearing scale affected richness and lake occupancy, the 2 strongest being amphipod density (discussed below) and lake area. Of the 2 types of breeding habitat, high-quality brood-rearing lakes are likely much rarer than are good nesting sites in the boreal forest, and our results likely reflect the prioritization of the rarer habitat during selection. For example,

just 17% of our study lakes contained 70% of amphipods collected during sampling. Likewise, the large lakes preferred for rearing broods are much less common in the boreal forest than are small ponds and semi-perennial wetlands. Terrestrial nesting habitats, however, are abundant, especially in the subarctic boreal forest where land development is relatively minimal. Our study site, the Yukon Flats basin, itself comprises 2.6 million ha of pristine boreal forest. This situation differs markedly from the Prairie Potholes Region, in which similar research has documented a significant influence of nesting habitats on brood occupancy (Walker et al. 2013). The Prairie Potholes Region, however, is a highly modified landscape where most of the lake margins have been converted to agriculture, severely limiting the availability of suitable nesting habitats.

We also hypothesized that waterbird chicks would require refugia from predators, especially during their first month when buoyancy, strength, and lung capacity limits their ability to escape via diving. Accordingly, we predicted that richness and lake occupancy by broods would be positively related to emergent vegetation because it provides cover from predators. This prediction was true for grebes, which typically nest within emergent vegetation, compiling mud and vegetation to keep their nest above water (Ulfvens 1988). However, because they nest and rear their broods on the same lake, we cannot determine whether their positive association with emergent vegetation is due to its function as predator cover, nesting habitat, or both. Regardless, emergent vegetation is clearly important for grebe reproduction on boreal lakes. Conversely, species richness was negatively related to emergent vegetation extent, whereas lake occupancy of scaup and scoter ducklings was unrelated. For emergent values >1.0, at which point the area of emergent vegetation exceeds that of open water, richness was clearly lower. Such lakes are largely overgrown with emergent vegetation and often avoided by diving waterbird species that require open water for foraging (Anteau and Afton 2009, Walker et al.

2013). Additionally, emergent vegetation was present on nearly every lake in our study area and encompassed >25% of lake area, on average. Thus, emergent vegetation was likely sufficiently common to have little influence on lake selection by scaup and scoters, being overridden by more limiting ecological factors such as amphipod density.

Our third hypothesis was that more productive lakes, as defined by their relatively greater concentrations of nitrogen, phosphorus and chlorophyll *a*, would have higher species richness and probabilities of lake occupancy. The general mechanism is that greater nutrient levels stimulate more primary productivity, adding more overall energy to the lake system and thereby increasing its potential to support additional species and trophic levels (Waide et al. 1999, Dodson et al. 2000). Indeed, waterbird richness appeared positively related to all 3 measures of aquatic productivity, although the relationship was strongest for total phosphorus. In freshwater systems, phosphorus most commonly limits productivity, especially when nitrogen:phosphorus ratios (N:P) exceed 20 (Downing and McCauley 1992). Of our 72 study lakes, 53 had N:P ratios >20, suggesting that phosphorus was more commonly limiting than was nitrogen, and likely explaining phosphorus's stronger relationship with species richness.

For scaup, scoters, and grebes, however, probability of lake occupancy was unrelated to total nitrogen and phosphorus. Our total phosphorus (TP) concentrations were quite high relative to other boreal areas, with 65% of our lakes classified as eutrophic (TP of 24–96 µg/l) and 26% as hypereutrophic (TP >96 µg/l). Similarly, our total nitrogen concentrations were among the highest documented in the boreal forest (Lewis et al. 2014). Such high nitrogen and phosphorus concentrations are unlikely to provide severe limits on aquatic productivity, despite the skewed N:P ratios, thus having limited influence on single species occupancy models. Similarly, lake occupancy by scaup and scoters was unrelated to chlorophyll levels, whereas that of grebes was

negatively related. Grebes are highly visual predators and may thus avoid lakes with elevated chlorophyll concentrations because of the decreased water clarity (Heglund et al. 1994).

Our final hypothesis was that aquatic invertebrate abundance would be an important determinant of lake occupancy and species richness because of the high food demands of rapidly growing waterbird chicks. This hypothesis was largely supported; aside from lake area, amphipod density was the best predictor of species richness, as well as lake occupancy of scaup, scoter, and grebe broods. However, none of the other invertebrate orders (Diptera, Gastropoda, Hemiptera, Odonata) influenced occupancy and richness. Indeed, the strong, positive response of waterbird chicks to amphipod density is all the more significant when compared to their lack of response to the other common aquatic invertebrates. Our amphipod results corroborate previous research highlighting the importance of amphipods in diets of scaup ducklings (Lindeman and Clark 1999, Fast et al. 2004). In the boreal forest of western Canada, amphipods comprised 57% of food items in stomachs of scaup ducklings (Bartonek and Murdy 1970). Amphipods have also been noted as a potentially important food for scoters and grebes in the boreal forest (Haszard and Clark 2007, Kuczynski and Paszkowski 2010). Ours is the first known study, however, to have demonstrated the influence of amphipods on species richness of waterbird chicks, as richness increased approximately 5-fold across the range of amphipod densities, from 2–3 to >15 species.

Why was amphipod density, and not densities of the other invertebrate groups, an important predictor of richness and lake occupancy for waterbird chicks? The simplest explanation is that chicks are feeding solely on amphipods. However, most waterbird species have diverse diets that commonly include each of the invertebrate orders considered in our study (Bartonek and Murdy 1970, Kuczynski and Paszkowski 2010). As well, >5 invertebrate orders

were found in stomachs of scaup and grebe chicks from our study lakes. Rather, the extreme densities, nutritional value, behavior, and size of amphipods likely make them highly important prey for waterbird chicks on boreal lakes. Although mean Diptera densities were higher in our study lakes, amphipod densities had the highest maximal values, occasionally reaching densities >4,000/m^3. Such exceptional densities likely provided a food source that was easy to locate and capture, especially for young chicks that are inexperienced foragers. In terms of size, average length of amphipods (4.22 mm) was not significantly larger than for the other orders (Diptera: 4.31 mm, Gastropoda: 2.98 mm, Hemiptera: 3.48 mm, Odonata: 5.71 mm); however, with the exception of Odonata, biomass of amphipods is generally greater per unit length than for the other orders (Gardner et al. 1985). In particular, Chironomid larvae, which were the most abundant Dipteran, have nearly 100-fold lower biomass per unit length than do amphipods (Gardner et al. 1985). The energy content of common freshwater amphipods *Gammarus* spp. (3.8 kcal/g) and *Hyallela* spp. (4.9 kcal/g) also compares favorably to other abundant invertebrates in our study lakes, including Gastropod snails (families Lymnaeidae [1.0 kcal/g] and Planorbidae [1.0 kcal/g]), Hemiptera (Corixidae [5.2 kcal/g]), and Chironomid larvae (4.6 kcal/g; Fredrickson and Reid 1988). Behaviorally, amphipods commonly swim freely in the water column, which likely makes them easier for waterbird chicks to discover and capture than more stationary invertebrates. For example, Odonata larvae and Gastropods are typically attached to aquatic vegetation, providing fewer visual movement cues to foraging chicks.

Although amphipods were clearly an important determinant of chick occupancy, we also observed scaup and grebe chicks on lakes without amphipods, albeit at a much lower rate of occupancy than on lakes with amphipods. This indicates that waterbird chicks may subsist on diets that do not include amphipods, instead relying on other common invertebrate taxa such as

Diptera or Gastropoda. Previous research on staging scaup along the Mississippi flyway, however, suggested that amphipods have a large, positive influence on scaup body condition (Anteau and Afton 2004). Accordingly, broods of scaup and other waterbird species may experience reduced fitness when occupying lakes without amphipods. This will be explored in future research efforts, in which we will compare body mass of scaup ducklings across a gradient of amphipod densities, from lakes without amphipods to those harboring superabundant densities. Finally, amphipod densities from our study site ($\bar{x}$ = 220/m^3) are markedly high in comparison to those reported elsewhere (e.g., Walsh et al. 2006, Anteau and Afton 2008), although data from boreal lakes are generally lacking. Correspondingly high amphipod densities were documented in lakes of the Canadian Arctic following artificial fertilization, as benthic densities increased from <100/m^2 to nearly 500/m^2 upon nitrogen and phosphorus additions (Jorgenson et al. 1992). This same concept may apply to our study lakes, most of which qualify as eutrophic or hypereutrophic given their elevated levels of total nitrogen ($\bar{x}$ = 2,597 µg/l) and phosphorus ($\bar{x}$ = 311 µg/l). These extremely high nitrogen and phosphorus concentrations may stimulate elevated levels of primary productivity, which may, in turn, transfer upward to primary consumers such as amphipods, thereby supporting higher amphipod densities. Moreover, the lack of fish in our study lakes may allow for elevated amphipod densities; fish are major predators of amphipods and fishless lakes support more abundant populations of aquatic invertebrates because piscine predation is relaxed (Bendell and McNicol 1987, Anteau and Afton 2008).

2.7 Management Implications

Our data indicate that, when aiming for maximal species richness and brood production, managers of undeveloped boreal areas prioritize conservation and management of brood-rearing

lakes above that of nesting habitat. High quality brood-rearing lakes, defined by their high productivity and abundant invertebrates, are much rarer, and thus more constraining, than are quality nesting habitats, which are likely abundant in the boreal. Our analysis also clearly identified lake size and amphipod density as the most important factors relating to species richness and distributions of waterbird broods. Moreover, the magnitude of these relationships were strikingly consistent among all 3 study species (scaup, scoters, grebes), as well as richness of 17 waterbird species, suggesting that lake area and amphipod density are intrinsic variables of high conservation value for the boreal forest in general. Amphipods were patchily distributed in our study lakes, being absent altogether on 25% of lakes and in low density on many others. As such, boreal lakes with abundant amphipod populations should be prioritized for conservation and monitoring, especially those with surface areas >25 ha. Lakes selected for conservation in this manner, as opposed to those based solely on waterbird abundance, have a high probability of sustained conservation value because their use by broods is firmly based on established ecological relationships (Hansen and DeFries 2007).

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2.10 Figures

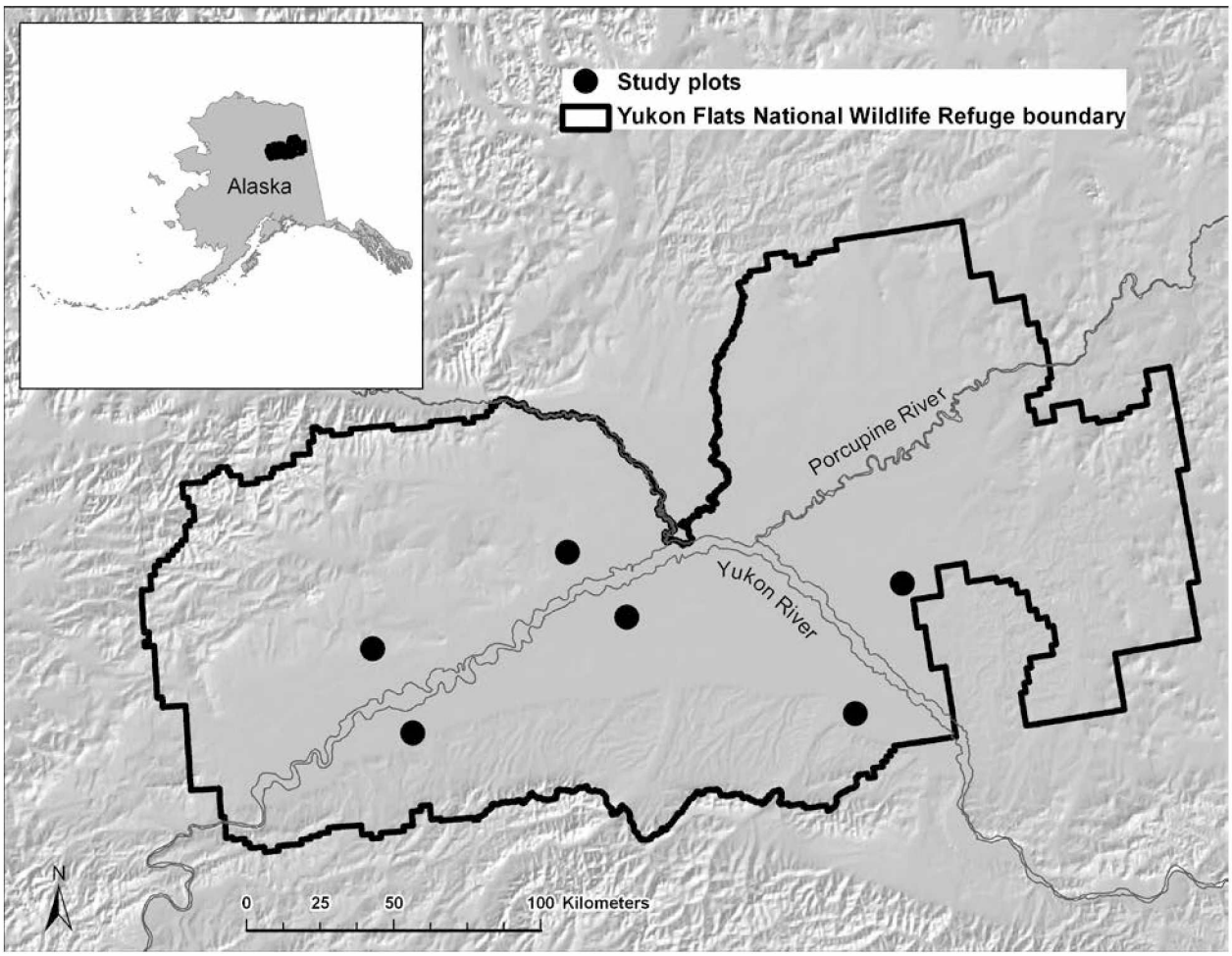

Figure 2-1. Map of the study area in the Yukon Flats National Wildlife Refuge, Alaska, showing the location of the 6 study plots.

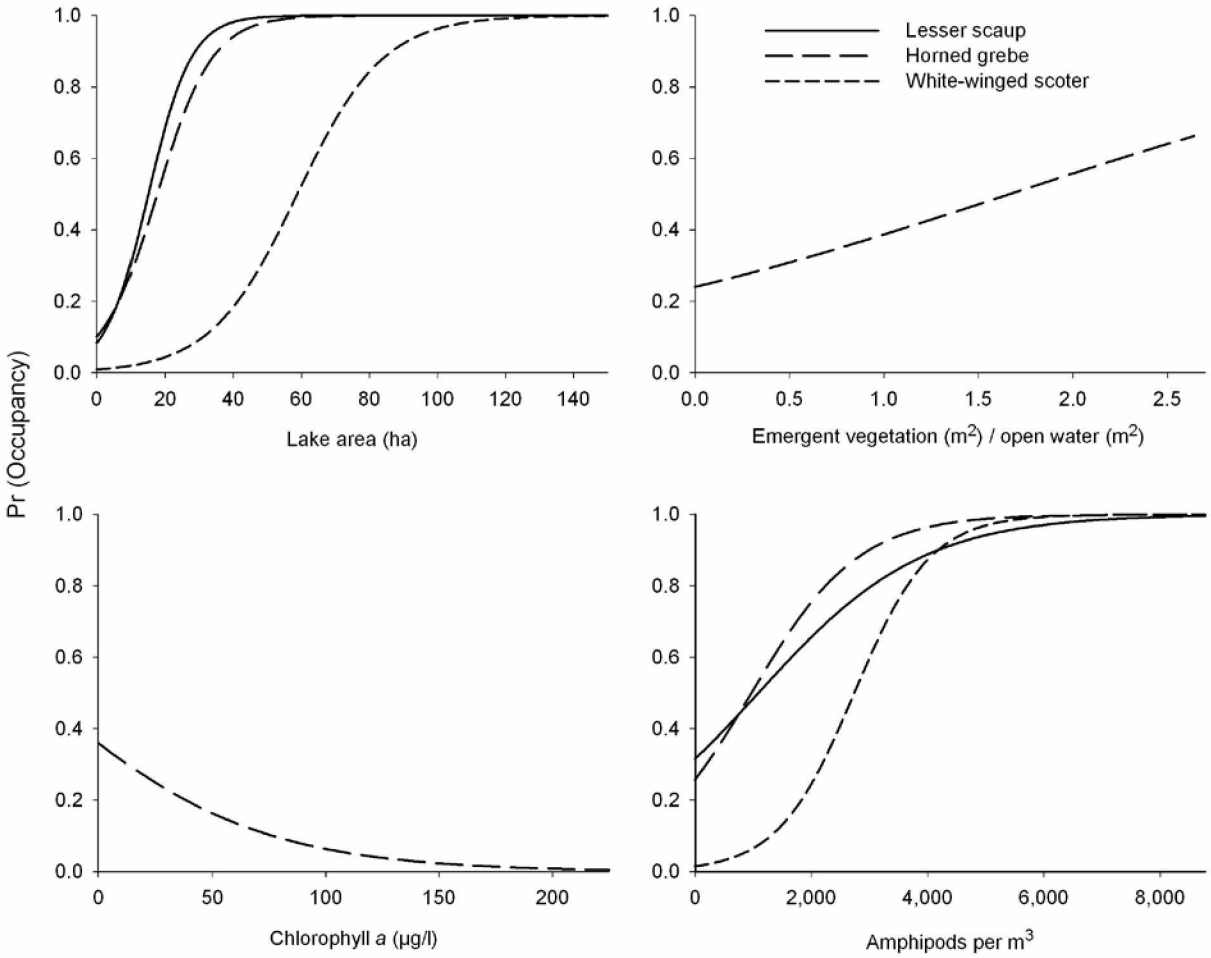

Figure 2-2. Probability (Pr) of lake occupancy for broods of lesser scaup, horned grebe, and white-winged scoters relative to covariates in the Yukon Flats, Alaska, 2010–2012. Graphs are restricted to the observed range of covariate values. We show only strongly supported relationships, in which 95% confidence intervals did not overlap 0. We omitted confidence intervals for clarity of presentation, but report them in Table 3.

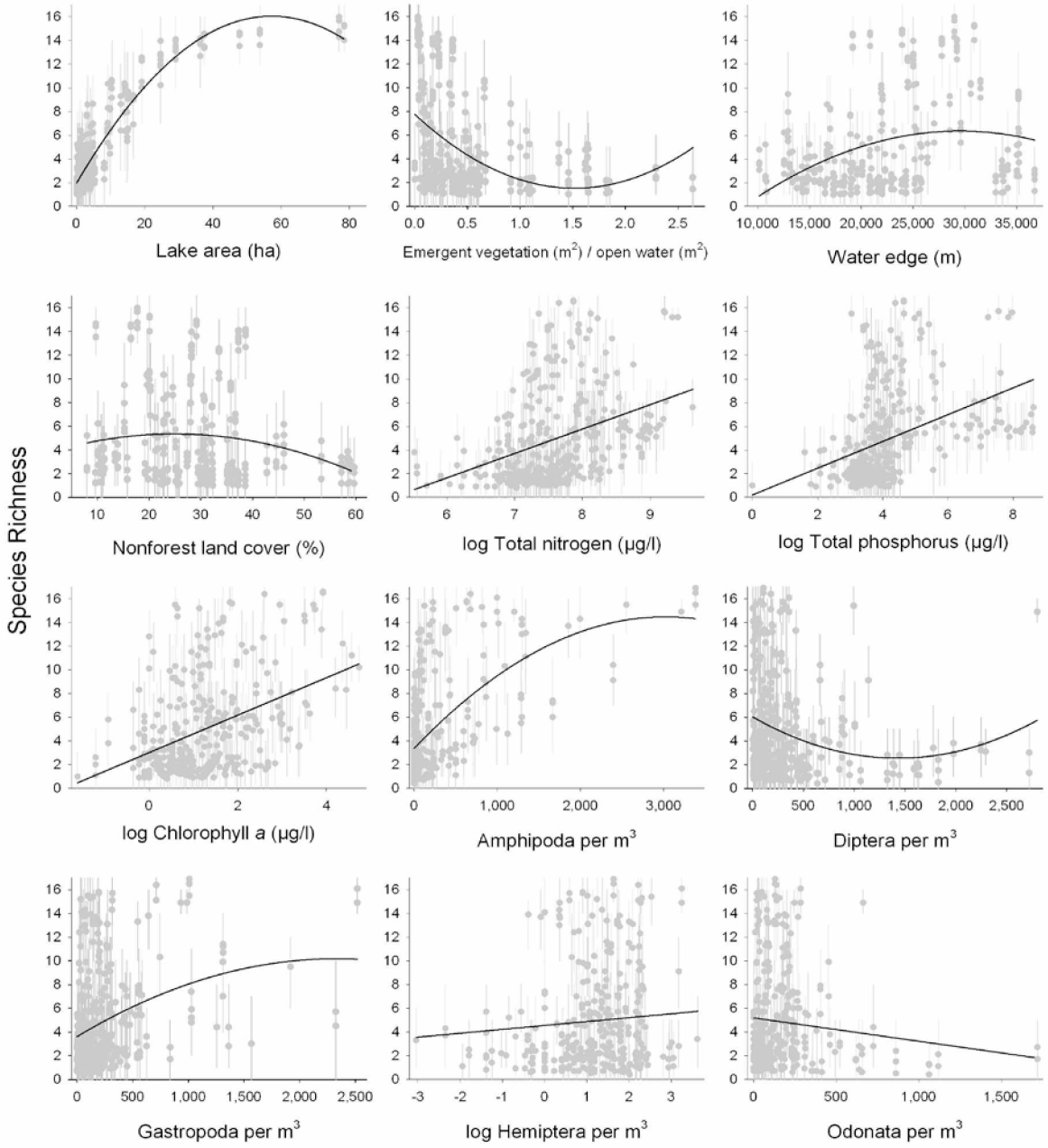

Figure 2-3. Patterns of species richness relative to covariates describing physical attributes of brood-rearing lakes (lake area, emergent vegetation/lake area), nesting habitats (water edge, non-forest land cover), water chemistry (total nitrogen, total phosphorus, chlorophyll a), and aquatic invertebrate density (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata) in the Yukon Flats, Alaska, 2010–2012. Richness is the number of species of waterbird chicks as estimated from multi-species occupancy models that accounted for non-detected species. Each data point represents survey-specific posterior means of species richness with associated 95% credible intervals. Solid trend lines represent approximate relationships between richness and covariates as estimated from regression models.

2.11 Tables

Table 2-1. Summary statistics for covariates used in models describing occupancy probability and species richness of waterbird broods in the Yukon Flats, Alaska, 2010–2012.

Covariate	Min.	Quartile 1	Quartile 3	Max.	Median	Mean	SD
Nonforest cover (%)	8.02	20.11	33.50	59.61	27.34	27.73	11.67
Water edge (m)	10,132.19	17,406.72	98,460.14	51,237.06	21,929.36	22,594.84	7,090.07
Lake area (ha)	0.04	0.65	9.85	201.88	3.05	11.22	2.54
Emergent vegetation (m^2) / open water (m^2)	0	0.15	0.62	2.64	0.36	0.55	0.57
Total nitrogen (µg/l)	230	1,250	2,782.5	22,580	1,770	2,596.98	2,618.02
Total phosphorus (µg/l)	1	32	92	6,216	47	310.99	866.20
Chlorophyll *a* (µg/l)	0.20	1.80	6.75	559.10	3.2	8.49	29.76
Amphipoda (no./m^3)	0	0	184.61	8,773.06	19.98	219.51	598.59
Diptera (no./m^3)	0	52.95	361.99	5,908.88	142.49	371.86	671.52
Gastropoda (no./m^3)	0	34.18	222.64	5,413.54	98.45	212.77	393.52
Hemiptera (no./m^3)	0	27.92	138.40	2,168.59	69.56	123.23	215.66
Odonata (no./m^3)	0	24.07	162.46	1,654.73	64.27	125.40	189.18

Table 2-2. Pearson correlation matrix for covariates used in models describing occupancy probability and species richness of waterbird broods in the Yukon Flats, Alaska, 2010–2012. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), Chlorophyll *a* (Chla), and density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata).

Covariate	Non-forest	Edge	Area	Veg	TN	TP	Chla	Amphipoda	Diptera	Gastropoda	Hemiptera	Odonata
Non-forest	1											
Edge	0.54	1										
Area	–0.13	0.46	1									
Veg	–0.14	–0.22	–0.27	1								
TN	–0.21	–0.24	0.07	–0.15	1							
TP	–0.13	–0.12	–0.02	0.01	0.57	1						
Chla	–0.10	0.03	0.01	–0.05	0.24	0.45	1					
Amphipoda	0.09	0.27	0.44	–0.19	–0.01	–0.06	0.01	1				
Diptera	0.01	–0.05	–0.04	0.10	0.36	0.32	0.04	–0.02	1			
Gastropoda	0.01	0.08	0.21	–0.08	0.08	0.14	–0.05	0.19	0.09	1		
Hemiptera	–0.08	0.01	0.05	–0.06	0.44	0.29	0.26	–0.01	0.37	0.03	1	
Odonata	0.13	0.04	–0.04	0.11	–0.14	–0.10	–0.08	0.11	0.20	0.21	0.00	1

Table 2-3. Model-averaged parameter estimates (est.) and unconditional standard errors from models evaluating variation in probability of lake occupancy by lesser scaup, white-winged scoter, and horned grebe broods in the Yukon Flats, Alaska, 2010–2012. We indicate estimates with 95% confidence intervals that did not include 0 with an asterisk (*). Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen, total phosphorus, Chlorophyll *a*, density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

Covariate	Lesser scaup		White-winged scoter		Horned grebe	
	Est.	SE	Est.	SE	Est.	SE
Stage 4: Year[a]						
Year 2011	–1.27*	0.43*	–1.30	0.87	–0.22	0.35
Year 2012	–0.43	0.42	–0.59	0.92	0.41	0.37
Stage 3: Aquatic invertebrates						
Amphipoda	0.63*	0.28*	1.16*	0.34*	0.74*	0.23*
Diptera	–0.10	0.22	–0.60	0.57	–0.21	0.24
Gastropoda	0.22	0.17	0.01	0.44	0.20	0.15
Hemiptera	–0.04	0.20	–0.98	0.60	0.03	0.22
Odonata	–0.12	0.23	0.02	0.72	–0.11	0.17
Stage 2: Water chemistry						
Total phosphorus	–0.20	0.29	–0.32	0.68	0.04	0.21
Total nitrogen	–0.01	0.17	0.43	0.44	–0.24	0.22
Chlorophyll *a*	0.09	0.17	0.22	0.32	–0.73*	0.34*
Stage 1: Lake and Landscape						
Area	4.60*	0.77*	2.11*	0.45*	3.28*	0.60*
Veg	–0.23	0.24	–0.70	1.18	0.40*	0.15*
Edge	0.11	0.24	–0.12	0.45	–	–
Non-forest	–0.14	0.22	–0.13	0.38	–	–

[a] Reference value for categorical parameter year is 2010.

Table 2-4. Difference in corrected Akaike's Information Criterion (ΔAIC_c) values from candidate models evaluating variation in species richness of waterbird broods in the Yukon Flats, Alaska, 2010–2012. We fit 4 models, listed in order of number of parameters (K), to each covariate: intercept, linear, log-linear, and quadratic models. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (Veg), total nitrogen (TN), total phosphorus (TP), Chlorophyll *a* (Chla), and density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata).

Covariate	Intercept model ($K = 2$)	Linear model ($K = 3$)	Log model ($K = 3$)	Quadratic model ($K = 4$)
Non-forest	7.74	4.63	7.73	0
Edge	33.39	10.59	7.13	0
Area	764.04	297.30	463.41	0
Veg	68.27	26.22	29.09	0
TN	62.18	6.48	0	5.15
TP	89.40	58.69	0	38.08
Chla	72.58	20.18	0	2.53
Amphipoda	153.99	15.02	60.44	0
Diptera	8.85	5.35	2.48	0
Gastropoda	41.44	1.36	18.04	0
Hemiptera	7.92	2.50	0	1.07
Odonata	2.82	2.38	0	1.64

2.12 Appendix

Appendix 2.A. Model selection results from models evaluating variation in probability of lake occupancy by broods of lesser scaup, white-winged scoters, and horned grebes.

Table 2.A-1. Model selection results for candidate models evaluating variation in probability of lake occupancy by lesser scaup broods in the Yukon Flats, Alaska, 2010–2012. We selected models sequentially in 4 stages, with the best-supported model from each lower stage serving as a template for the next stage. We ranked models in each stage in order of difference in corrected Akaike's Information Criterion (ΔAIC_c) and we also report number of parameters (K) and model weights (w_i). We excluded all models from the reported set that did not result in lower AIC_c scores upon addition of 1 covariate, with the exception of the simplest models at each stage. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), Chlorophyll *a* (Chla), density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

Model	ΔAIC_c	K	w_i
Stage 4: Year covariates			
Area + Amphipoda + Year	0	8	0.94
Area + Amphipoda	5.68	6	0.06
Stage 3: Aquatic invertebrate covariates			
Area + Amphipoda	0	6	0.45
Area	1.77	5	0.19
Area + Gastropoda	2.30	6	0.14
Area + Diptera	3.52	6	0.08
Area + Hemiptera	3.75	6	0.07
Area + Odonata	3.79	6	0.07
Stage 2: Water chemistry covariates			
Area	0	5	0.44
Area + TP	1.51	6	0.21
Area + Chla	1.79	6	0.19
Area + TN	2.04	6	0.16

Table 2.A-1 (continued)

Model	ΔAIC_c	K	w_i
Stage 1: Lake and landscape covariates			
Area	0	5	1
Veg	69.42	5	0
Edge	86.07	5	0
Non-forest	98.96	5	0
Null	100.11	4	0

Table 2.A-2. Model selection results for candidate models evaluating variation in probability of lake occupancy by white-winged scoter broods in the Yukon Flats, Alaska, 2010–2012. We selected models sequentially in 4 stages, with the best-supported model from each lower stage serving as a template for the next stage. We ranked models in each stage in order of difference in corrected Akaike's Information Criterion (ΔAIC_c) and we also report number of parameters (K) and model weights (w_i). We excluded all models from the reported set that did not result in lower AIC_c scores upon addition of 1 covariate, with the exception of the simplest models at each stage. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), Chlorophyll *a* (Chla), density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

Model	ΔAIC_c	K	w_i
Stage 4: Year covariates			
Area + TP + Amphipoda + Hemiptera	0	8	0.71
Area + TP + Amphipoda + Hemiptera + Year	1.81	10	0.29
Stage 3: Aquatic invertebrate covariates			
Area + TP + Amphipoda + Hemiptera	0	8	0.63
Area + TP + Amphipoda	1.09	7	0.36
Area + TP + Hemiptera	11.32	7	0
Area + TP	13.04	6	0
Area + TP + Odonata	15.00	7	0
Area + TP + Gastropoda	15.07	7	0
Area + TP + Diptera	15.209	7	0
Stage 2: Water chemistry covariates			
Area + TP	0	6	0.62
Area	2.05	5	0.22
Area + TN	3.70	6	0.10
Area + Chla	4.75	6	0.06
Stage 1: Lake and landscape covariates			
Area	0	5	1
Edge	46.38	5	0
Non-forest	50.76	5	0
Veg	51.47	5	0
Null	57.05	4	0

Table 2.A-3 Model selection results for candidate models evaluating variation in probability of lake occupancy by horned grebe broods in the Yukon Flats, Alaska, 2010–2012. We selected models sequentially in 4 stages, with the best-supported model from each lower stage serving as a template for the next stage. We ranked models in each stage in order of difference in corrected Akaike's Information Criterion (ΔAIC_c) and we also report number of parameters (K) and model weights (w_i). We excluded all models from the reported set that did not result in lower AIC_c scores upon addition of 1 covariate, with the exception of the simplest models at each stage. Covariates include percent of non-forest cover (non-forest), total distance of water edges (edge), lake area (area), emergent vegetation (veg), total nitrogen (TN), total phosphorus (TP), Chlorophyll *a* (Chla), density of 5 invertebrate orders (Amphipoda, Diptera, Gastropoda, Hemiptera, Odonata), and year (2010, 2011, 2012).

Model	ΔAIC_c	K	w_i
Stage 4: Year covariates			
Area + Veg + TN + Chla + Amphipoda	0	9	0.61
Area + Veg + TN + Chla + Amphipoda + Year	0.92	11	0.39
Stage 3: Aquatic invertebrate covariates			
Area + Veg + TN + Chla + Amphipoda	0	9	0.96
Area + Veg + TN + Chla	8.81	8	0.01
Area + Veg + TN + Chla + Diptera	9.31	9	0.01
Area + Veg + TN + Chla + Gastropoda	9.97	9	0.01
Area + Veg + TN + Chla + Hemiptera	10.85	9	0
Area + Veg + TN + Chla + Odonata	10.86	9	0
Stage 2: Water chemistry covariates			
Area + Veg + TN + Chla	0	8	0.45
Area + Veg + Chla	0.24	7	0.40
Area + Veg + TN	3.21	7	0.09
Area + Veg	4.56	6	0.05
Area + Veg + TP	6.27	7	0.02
Stage 1: Lake and landscape covariates			
Area + Veg	0	6	0.76
Area	2.34	5	0.24
Veg	72.35	5	0
Null	75.74	4	0

Appendix 2.B. List of waterbird species for which we observed broods during surveys.

Table 2.B-1. Number of chicks observed per waterbird species during surveys conducted on boreal lakes of the Yukon Flats, Alaska, 2010–2012. We summed number of chicks across years, lakes, and surveys for each species. Estimates of species richness are based solely on the species listed herein.

Species	Number observed
Pacific loon (*Gavia pacifica*)	47
Red-necked grebe (*Podiceps grisegena*)	155
Horned grebe (*Podiceps auritus*)	1,875
Trumpeter swan (*Cygnus buccinator*)	53
Mallard (*Anas platyrhynchos*)	1,179
Northern pintail (*Anas acuta*)	822
American wigeon (*Anas Americana*)	3,177
Northern shoveler (*Anas clypeata*)	776
Green-winged teal (*Anas crecca*)	951
Canvasback (*Aythya valisineria*)	466
Ring-necked duck (*Aythya collaris*)	295
Lesser scaup (*Aythya affinis*)	3,961
Surf scoter (*Melanitta perspicillata*)	56
White-winged scoter (*Melanitta fusca*)	1,206
Common goldeneye (*Bucephala clangula*)	28
Barrow's goldeneye (*Bucephala islandica*)	2
Bufflehead (*Bucephala albeola*)	90

Chapter 3

Pronounced chemical response of Subarctic lakes to climate-driven losses in surface area[1]

3.1 Abstract

Losses in lake area have been observed for several Arctic and Subarctic regions in recent decades, with unknown consequences for lake ecosystems. These reductions are primarily attributed to two climate-sensitive mechanisms, both of which may also cause changes in water chemistry: *i*) increased imbalance of evaporation relative to inflow, whereby increased evaporation and decreased inflow act to concentrate solutes into smaller volumes, and *ii*) accelerated permafrost degradation, which enhances sublacustrine drainage while simultaneously leaching previously frozen solutes into lakes. We documented changes in nutrients (total nitrogen [TN], total phosphorus [TP]) and ions (calcium, chloride, magnesium, sodium) over a 25 year interval in shrinking, stable, and expanding Subarctic lakes of the Yukon Flats, Alaska. Concentrations of all six solutes increased in shrinking lakes from 1985–1989 to 2010–2012, while simultaneously undergoing little change in stable or expanding lakes. This created a present-day pattern, much weaker or absent in the 1980s, in which shrinking lakes had higher solute concentrations than their stable or expanding counterparts. An imbalanced evaporation-to-inflow ratio (E/I) was the most likely mechanism behind such changes; all four ions, which behave semi-conservatively and are prone to evapoconcentration, increased in shrinking lakes and, along with TN and TP, were positively related to isotopically-derived E/I estimates. Moreover, the most conservative ion, chloride, increased >500% in shrinking lakes. Conversely,

[1] Lewis, T.L., M.S. Lindberg, J.A. Schmutz, P.J. Heglund, J. Rover, J.A. Koch, and M.R. Bertram. 2015. Pronounced chemical response of Subarctic lakes to climate-driven losses in surface area. Global Change Biology 21:1140–1152.

only TP concentration was related to probability of permafrost presence, being highest at intermediate probabilities. Overall, the substantial increases of nutrients (TN >200%, TP >100%) and ions (>100%) may shift shrinking lakes towards overly eutrophic or saline states, with potentially severe consequences for ecosystems of northern lakes.

3.2 Introduction

Lakes and ponds are dominant features of Arctic and Subarctic landscapes, often accounting for more than half of total surface area (Rautio *et al.,* 2011). These waterbodies provide numerous ecosystem services, including long-term storage of substantial carbon stocks (Walter Anthony *et al.*, 2014), and important habitat for the region's wildlife (Vincent *et al.,* 2013). Temperature increases associated with global climate change are especially amplified at northern high-latitudes due to snow and ice albedo feedbacks, having already increased by at least twice the global average warming (New *et al.,* 2011). These substantial temperature increases have been linked to long-term shifts in lake water balance, including a net loss of lake surface area in Arctic and Subarctic regions of Alaska (Riordan *et al.,* 2006: Rover *et al.,* 2012), Canada (Smol & Douglas 2007; Carroll *et al.,* 2011), and Siberia (Smith *et al.,* 2005), with unknown consequences for lake ecosystems.

Two of the primary climate-driven mechanisms deemed responsible for losses of surface area in northern lakes are (*i*) increasingly imbalanced evaporation-to-inflow ratios, whereby some combination of increased evaporative water loss and decreased water inputs cause surface area reductions, and (*ii*) accelerated permafrost degradation, in which newly thawed soils enhance sublacustrine drainage of lake waters. Shallow lakes and ponds, a common lake type of northern landscapes, are susceptible to evaporation because of their high surface area to depth

ratios (Smol & Douglas 2007). Moreover, rates of evaporation have likely increased with climate change due to warmer air and water temperatures and longer ice-free seasons (Magnuson *et al.,* 2000; Surdu *et al.,* 2014). To prevent lakes from shrinking, evaporative losses must be balanced by water inputs, of which snowmelt is a crucial source at such northerly latitudes. Yet, climate models predict decreased snowfall for many Arctic and Subarctic regions, further exacerbating lake drawdown (Bouchard *et al.,* 2013). Climate change has also increased rates of permafrost degradation, especially at Subarctic latitudes where permafrost temperatures are near 0°C and thus vulnerable to thawing with small changes in climate (Jorgenson *et al.,* 2001). Many northern lakes persist, despite their low water volumes, largely due to sublacustrine permafrost, which retards water infiltration. However, vertical permafrost degradation below lakes may create new subsurface pathways for lake water movement and increase storage capacity of subsurface soils, potentially causing lakes to shrink (Jepsen *et al.,* 2013a; Necsoiu *et al.,* 2013).

Shrinking shallow lakes may be susceptible to changes in their water chemistry, including eutrophication and salinization. Increased evaporation of lake water, if not balanced by concurrent increases to water inputs, concentrates nutrients and ions into smaller water volumes (Smol & Douglas 2007). Lakes that lose water in this manner tend to exhibit greater increases in salinity than those that lose water largely via subsurface infiltration (Fritz 1996; Koch *et al.,* 2014). Permafrost degradation may also affect lake water chemistry, mostly through nutrient loading. As the climate warms, large stores of frozen organic matter in permafrost become available for decomposition and mineralization, with potential for hydrologic export to lakes (Petrone *et al.,* 2006; Wrona *et al.,* 2006). Such processes, although poorly described for lakes, have been associated with increased concentrations of dissolved and particulate carbon, nitrogen, and phosphorus in Arctic and Subarctic streams, especially in areas underlain with unstable,

discontinuous permafrost (Jones *et al.,* 2005; Frey *et al.,* 2007; Harms & Jones 2012). Importantly, effects of eutrophication and salinization extend beyond water quality, potentially reshaping the fundamental ecological structure and biota of affected lakes. In particular, productivity and species richness of lakes are strongly influenced by nutrient and salt concentrations, with generally adverse consequences as lakes shift towards eutrophic and/or saline states (Hammer 1986; Dodson *et al.,* 2000).

To date, changes in water chemistry in shrinking northern lakes remain largely unknown, especially at Subarctic sites with discontinuous permafrost cover. Our area of study is situated in the Yukon Flats (Fig. 1), a large boreal lowland in Subarctic Alaska with more than 40,000 lakes and ponds, most of which reside in shallow basins. Although the area receives little annual precipitation (17–24 cm [rain + snow]), lakes persist due to an impermeable permafrost layer that restricts drainage and short ice-free seasons (~5 months) that limit evaporation (Ford & Bedford 1987). As such, climatic-driven changes in precipitation, evaporation rate, and permafrost stability have the potential to strongly influence water levels of Yukon Flats lakes. From 1979 to 2009, 9% of Yukon Flats lakes decreased in surface area extent, 86% remained stable, and 5% increased, with the region's total lake surface area experiencing a net loss (Rover *et al.,* 2012). This inherent heterogeneity provided an ideal study system, allowing us to compare water chemistry across closely located and ecologically similar lakes with opposing surface area trends. Specifically, we examined changes in water chemistry in shrinking, stable, and expanding lakes of the Yukon Flats from 1985–1989 to 2010–2012, making use of chemical data from the 1980s that benchmarked past lake conditions. We looked at changes in two aquatic nutrients of high biologic importance (nitrogen, phosphorus) and four conservative or semi-conservative ions (calcium, chloride, magnesium, sodium), expecting that these solutes would increase

disproportionately in shrinking relative to stable or expanding lakes. We used semi-conservative ions because, relative to nutrients, they are largely unreactive and minimally used by most lacustrine organisms; hence, their concentrations are highly influenced by evaporation-to-inflow ratios (Schemel *et al.,* 2006; Waiser 2006). Finally, to provide insight into possible mechanisms for changes in water chemistry, we examined variation in nutrient and ion concentrations in relation to evaporation-to-inflow ratios, predicting a positive relationship, and probability of permafrost presence, predicting increased concentrations at intermediate to high probabilities.

3.3 Materials and Methods

Our research was conducted on 6 randomly selected study plots spread across the Yukon Flats (66.0°N, 144.2°W to 66.6°N, 148.3°W) and used for previous limnological research (Fig. 1; Heglund and Jones 2003). Study plots measured 10.36 km^2 and contained 7–17 lakes, for a total of 74 study lakes. Lakes varied in size from 0.1 to >200 ha, but were uniformly shallow with saucer-shaped basins that were largely closed, with few well-defined inlets or outlets (Table 1). This combination of shallow depth and lack of outlets precluded fish populations in all lakes. Study plots were underlain by continuous and discontinuous permafrost and generally had low landscape relief (<50 m). Mixed boreal forest covered much of the area and was dominated by black (*Picea mariana*) and white spruce (*P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.).

Lake water chemistry was originally sampled in 1985–1989 (Heglund & Jones 2003). At that time, each lake was sampled 1–2 times per month (Jun–Sept) in 2 of 5 years, with the exception of 15 lakes that were sampled in ≥3 years. We re-sampled these same lakes in 2010–2012 using identical water sampling methods, and each lake was sampled 1–2 times per month

(Jun–Aug) in 2 of 3 years, except for 17 lakes that were sampled in all 3 years. During both periods, we collected 8 liters of water from near the lake's center point and 25 cm below the surface. Water samples were used to measure concentrations (mg l^{-1}) of total nitrogen (TN), total phosphorus (TP), calcium (Ca), chloride (Cl), magnesium (Mg), and sodium (Na). We used three 5 ml aliquots of unfiltered lake water for each TN and TP sample, with TN aliquots being acidified on-site with sulfuric acid; final TN and TP values are averages of the three aliquots. We used 60 ml of lake water filtered through Gelman A/E glass fiber filters (Gelman Filters, Pall Corporation, Port Washington, New York) for determination of ion (Ca, Cl, Mg, Na) concentrations. We immediately stored samples in the dark at cool temperatures following collection.

We replicated limnological laboratory procedures from 1985–1989 to 2010–2012, including use of the same lab (Jones Limnology Lab, University of Missouri, Columbia, MO). We determined TP concentrations by colorimetric measurement of orthophosphate following persulfate oxidation (method 4500-PE [APHA 1995]); TN concentrations by second-derivative spectroscopic analysis of persulfate-oxidized samples (Crumpton *et al.,* 1992); Cl concentrations by flow injection analysis and colorimetry (Pruefer 2007); and cation (Ca, Mg, Na) concentrations by using acid-preserved samples with an atomic absorption spectrophotometer or flame photometer (method 3120-B [APHA 1995]).

We used linear trends in lake surface area from 1979–2011, following methods described in Rover et al. (2012), to categorize each of our study lakes as shrinking (>20% decrease), stable (20% decrease to 20% increase), or expanding (>20% increase). Linear trends are lake-specific slope values derived from regression models that used time as the predictor variable and surface area as the response variable. We derived lake surface areas across the 32 year period from

Landsat data with a supervised decision tree classification model to differentiate water from terrestrial surfaces. Landsat data were selected for 22 unique acquisition dates that provided minimal cloud obstruction across a wide geographic area. These 22 dates covered 16 of the 32 years and the bulk of the ice-free season (8 May to 16 Sept), thus including sources of both intra- and inter-annual variation. We used conservative cut-offs for classifying our lakes as shrinking, stable, or expanding, rather than a continuous description, to account for the coarse resolution (30 m pixel) of Landsat imagery and the high-degree of inter-annual variation in surface area. Further, we restricted this classification to lakes with a surface area >1 ha (n = 55) because lakes smaller than this size could not be reliably classified using Landsat imagery.

Evaporation-to-inflow ratios (E/I) were calculated for each of our study lakes from Anderson et al. (2013) using an isotope mass balance model, thereby providing lake-specific measures of evaporative magnitude. The isotope mass balance model determines the amount of evaporation relative to inflow for each lake based on degree of offset between measured lake water isotope values ($\delta^{18}O$) and estimated isotopic composition of precipitation (Gibson & Edwards 2002). We collected lake water isotope samples at 58 lakes in July 2011 and 16 lakes in July 2012. These collections were temporally standardized to occur in July to minimize the effect of intra-annual variation on E/I values, while providing E/I estimates that roughly coincided with the annual peak of evaporation potential. We collected water isotope samples from just below the surface at the lake's midpoint, placed them in 30 ml polyethylene bottles with no air space, and analyzed them within 2 months of collection. Water samples were prepared for oxygen isotope ratio analysis by automated constant temperature equilibration with CO_2 coupled to an isotope ratio mass spectrometer. See Anderson et al. (2013) for a complete description of E/I estimation and isotope analyses for our study lakes.

We estimated the degree of permafrost around each lake based on a map of near-surface (top 123 cm) permafrost probability established for the Yukon Flats (Pastick *et al.,* 2013). Permafrost probabilities for this map were determined from field measurements, remote-sensed satellite imagery, and airborne electromagnetic resistivity surveys conducted from 2009–2010, and are expressed at a pixel resolution of 30 m. Permafrost probabilities are restricted to terrestrial surfaces, not including soils located below lakes. We created a 500 m buffer around each study lake and then averaged the probability values of all pixels contained within this buffer, thereby creating a composite permafrost probability for each study lake. These composite probabilities provide one near-surface permafrost value per lake, expressed on a 0–100% scale, and are used in all subsequent analyses.

Analyses

Our first analysis explored: 1) changes in water chemistry from 1985–1989 to 2010–2012, 2) differences in water chemistry between shrinking, stable, and expanding lakes, and 3) whether changes in water chemistry from 1985–1989 to 2010–2012 differed across shrinking, stable, and expanding lakes. We used concentrations of two nutrients (TN, TP) and four ions (Ca, Cl, Mg, Na) as our response variables for a series of general linear mixed models. We fit an identical set of six *a priori* models for each response variable. Our model set included a null intercept-only model; a model with ordinal date (intra-annual date on a scale of 1–366); a model with ordinal date and decade (defined categorically as 1980s vs. 2010s); a model with ordinal date and extent (defined categorically as shrinking, stable, or expanding); a model with ordinal date, decade, and extent; and a model with ordinal date and an interaction between decade and extent. We included ordinal date in every model, with the exception of the null model, to control for intra-annual

differences in chemistry, which was not our primary interest, but could confound our interpretation. We also included lake identity as a random effect in all models. This analysis was restricted to lakes with a surface area >1 ha (n = 55), from which we analyzed 801 water samples collected across the two decadal time periods.

Our second analysis examined potential mechanisms driving variation in water chemistry across lakes. This analysis was restricted to data from 2010–2012 because the main explanatory variables of interest, E/I and permafrost, were not measured during 1985–1989. We used the same set of response variables as described above: concentrations of TN, TP, Ca, Cl, Mg, and Na. For each response variable, we fit an identical set of nine *a priori* general linear mixed models. Explanatory variables included ordinal date, year (2010, 2011, 2012), lake area (derived from National Hydrography Dataset, U.S. Geological Survey), E/I, and permafrost (% probability of permafrost). Ordinal date and year constituted one model; moreover, we included these variables in all subsequent models, with the exception of the null model, to account for intra- and inter-annual variation in water chemistry. The remaining seven models included all additive combinations of lake area, E/I, and permafrost. Additionally, we used the quadratic form of permafrost in all models to account for non-linear relationships between permafrost and aquatic nutrient concentrations. We did not use extent (shrinking, stable, or expanding) as an explanatory variable because gross patterns between water chemistry and each of our explanatory variables (lake area, E/I, permafrost) should be general to all our study lakes; further, this allowed us to include data from 19 lakes that were too small (<1 ha) for accurate lake extent categorization, raising our sample size from 55 to 74 lakes. Our models included data from 535 water samples collected from 74 lakes, and lake identity was included as a random effect in all models.

All mixed models were run using the 'nlme' package in program R (Pinheiro *et al.*, 2013). We used an information-theoretic approach to data analysis and model selection (Burnham & Anderson 2002). Under this approach, there is no arbitrary, automatic decision to be reached regarding significance (e.g., $P < 0.05$). Rather, there is a focus on a small set of hypotheses in the form of candidate models, and the explanatory value of each model is assessed using multiple forms of quantitative evidence and careful consideration (Anderson & Burnham 2002). Specifically, we compared the relative fit of models within a candidate set using Akaike's information Criterion (AIC) and AIC weights (w_i), both of which indicate the relative likelihood of a model given the data. We converted raw AIC values to ΔAIC, with ΔAIC defined as the difference between the best-fitting model (smallest AIC) and each respective model in the candidate set; thus, $\Delta AIC = 0$ for the model of best fit. We considered all models with a $\Delta AIC \leq 2$ to have substantial support from the data (Burnham & Anderson 2002). We also included an intercept-only model in each model set to provide a null baseline for comparison.

We based inference of individual fixed effects on collective quantitative evidence provided by model selection metrics (ΔAIC, w_i) and precision of parameter estimates. When large standard errors (SE) indicated imprecise parameter estimates, the variable was deemed uninformative. We used model-averaged parameter estimates and unconditional standard errors (SE) when candidate model sets displayed selection uncertainty, with multiple models being supported by the data (Burnham & Anderson 2002). Otherwise, when a clear top model emerged, we used parameter estimates and SEs from the highest-ranked model. Finally, to determine the relative importance of E/I, permafrost, and lake area within each model set, we summed w_i across all models in which each variable appeared, producing a parameter likelihood for each variable scaled from 0 (not important) to 1 (highly important). This approach was

possible because of the balanced nature of our model sets, in which E/I, permafrost, and lake area each appeared in 4 of 9 models.

3.4 Results

Of the 55 lakes >1 ha, 18 were classified as shrinking, 33 as stable, and 4 as expanding. Parameter estimates indicated that concentrations of the two nutrients, TN and TP, increased in shrinking lakes from 1985–1989 to 2010–2012, while simultaneously undergoing relatively little change in stable and expanding lakes (Table 2). This created a present-day pattern, much weaker in the 1980s, in which shrinking lakes have markedly higher TN and TP concentrations than do stable and expanding lakes (Fig. 2). Concentration increases in shrinking lakes were of a substantial magnitude, as TN and TP increased >200% and >100%, respectively. Model selection results were unequivocal (Table 3), providing zero support for models lacking the decade*extent interaction ($w_i = 0$; $\Delta AIC > 30$); only models with this interaction term allowed for differential decadal variation across the three lake extent categories. Further, decade*extent parameter estimates for shrinking lakes (i.e., Decade*Extent: Shrink) were large, positive, and well-estimated, indicating substantial increases in TN and TP concentrations over time, while parameter estimates for stable and expanding lakes were poorly estimated with SEs that overlapped zero (Table 2).

Likewise, concentrations of all four ions (Ca, Mg, Na, Cl) increased in shrinking lakes from 1985–1989 to 2010–2012, while remaining relatively unchanged in stable and expanding lakes (Fig. 2). The most pronounced increase in shrinking lakes, exceeding 500%, was for Cl, generally considered the most conservative of the ions. Ca and Mg each increased approximately 50% in shrinking lakes, while Na also increased, but showed the most estimation uncertainty

with wide SEs (Table 2). All four ions had higher concentrations in shrinking than in stable and expanding lakes during 2010–2012, especially Cl. This pattern was much less evident during 1985–1989, although Mg and Na had higher concentrations in shrinking lakes dating back to this period (Fig. 2). Model selection results were again unequivocal (Table 3), with models lacking decade*extent receiving zero support ($w_i = 0$; $\Delta AIC > 11$) for Ca, Cl, and Mg, and negligible support ($w_i < 0.20$; $AIC \geq 2.66$) for Na.

E/I generally had a larger influence on solute concentrations than did permafrost or lake area. All six solutes were positively related to E/I, indicating a prevailing pattern whereby solute concentrations are higher on lakes with more evaporation relative to inflow. Of the nutrients, TN had the strongest relation to E/I (Table 4), increasing from 1–2 to >5 mg l^{-1} over the range of observed E/I values (Fig. 3). E/I appeared in all three top models (ΔAIC 0–1.81; Table 5) for TN and had a parameter likelihood of 1.0. Conversely, lake area and permafrost (Fig. 4) had no discernible influence on TN and received little model selection support (Table 5), with parameter likelihoods of 0.12 and 0.58, respectively. Model selection for TP also favored models with E/I over those with lake area and permafrost (Table 5); E/I had a parameter likelihood of 1.0, compared to 0.28 and 0.79 for lake area and permafrost, respectively. However, E/I was poorly estimated, with a SE that overlapped zero, while permafrost estimates were more precise, indicating that near-surface permafrost had a significant influence on TP concentrations (Table 4). Specifically, TP concentrations were highest at intermediate values of permafrost probability, especially in comparison to lakes with low permafrost probability (Fig. 4).

For all four ions, models with E/I received much stronger support than those with lake area and permafrost; E/I was in the top 2 models (ΔAIC 0–1.96; Table 5) and had a parameter likelihood of 1.0 for each ion, compared to parameter likelihoods of 0.28–0.44 and 0.15–0.26 for

lake area and permafrost, respectively. Concentrations of Ca, Cl, and Mg were positively related to E/I (Fig. 3), while Na was also positively related, but with wide SE that overlapped zero (Table 4). Semi-conservative Mg, in particular, showed marked increases in relation to E/I, increasing approximately 4-fold across the observed range of E/I values (Fig. 3). In contrast, near-surface permafrost probability had no influence on concentrations of all four ions, as indicated by a lack of model selection support (Table 5) and poorly-estimated parameter estimates with SEs that overlapped zero (Table 4). Concentrations of all four ions remained relatively constant across the range of observed permafrost probabilities (Fig. 4).

3.5 Discussion

While there exists a high degree of heterogeneity in surface area trends, with shrinking, stable, and expanding lakes commonly co-occurring, multiple recent studies have clearly identified several high latitude regions with net losses in lake surface area (Smith *et al.,* 2005; Riordan *et al.,* 2006; Carroll *et al.,* 2011; Roach *et al.,* 2011; Rover *et al.,* 2012). Herein we provide some of the first known documentation of the ecological consequences of declining surface waters, showing that shrinking lakes experience pronounced changes in water chemistry. Concentrations of six solutes, including nutrients and semi-conservative ions, increased considerably in shrinking Subarctic lakes over a 25 year interval, while simultaneously experiencing relatively little change in lakes with stable or expanding surface areas. This created a present-day pattern, much weaker or absent in the 1980s, in which shrinking lakes have markedly higher solute concentrations than their stable and expanding counterparts. This pattern was demonstrated across a large number of lakes (n = 55) and years (n = 8), minimizing the impact of outliers and suggesting a broad ecological pattern that overrides lake-specific and year-to-year variation.

Moreover, concentration increases in shrinking lakes were of a substantial magnitude, including increases of >500% for chloride, >200% for total nitrogen, and >100% for total phosphorus. Remarkably, these nutrient increases, though occurring in remote and otherwise pristine lakes, are of a magnitude comparable to those observed in artificially eutrophic waterbodies impacted by anthropogenic activities (Vitousek *et al.,* 1997; Smith *et al.,* 1999).

The large magnitude of nutrient increases in these shrinking lakes is even more noteworthy when considering their trophic status during their initial sampling in the 1980s. At that time, 70% of our study lakes qualified as eutrophic or hypereutrophic based on their high TN and TP concentrations (Heglund & Jones 2003). Such high initial nutrient loads require correspondingly large concentration increases to produce a detectable change, given that background levels of intra- and inter-annual variation are much higher. Nonetheless, nutrient concentrations more than doubled in these already nutrient-laden lakes, further ensuring their eutrophic status. These large nutrient increases also coincided with trends observed 10 years earlier for 5 of our shrinking study lakes. During 2001–2003, TN and ion concentrations in these 5 lakes had increased from 1980s levels by 160% and 30–60%, respectively (Corcoran *et al.,* 2009). These values fit within a continuum of steadily increasing solute concentrations from 1985–1989 to 2001–2003 to 2010–2012. TP concentrations from 2001–03, however, showed no change in these 5 lakes (Corcoran *et al.,* 2009), suggesting that our observation of increased TP levels in shrinking lakes may have occurred mainly during the most recent decade. Finally, the present-day pattern, whereby shrinking lakes have higher solute concentrations than stable and expanding lakes, was weak but not entirely absent in the 1980s, especially for Mg and Na. This suggests that a changing climate was actively influencing lake surface areas and solute concentration in the Yukon Flats dating back to the 1980s, which coincides with the beginning of

a general shift towards warmer temperatures and decreased snowfall for the region (Jepsen et al. 2013b).

Increasingly imbalanced E/I ratios appear to be a primary driver of long-term changes in water chemistry of our study lakes. First, concentrations of all four conservative or semi-conservative ions, which serve as indicators of E/I balance (Webster *et al.,* 1996; Waiser 2006), increased disproportionately in shrinking lakes from 1985–1989 to 2010–2012, with highly conservative chloride increasing the most. Chloride is an especially effective and widely used conservative tracer because it is biologically inactive and its catchment inputs are largely restricted to atmospheric deposition, thereby limiting the possible sources responsible for concentration increases (Hayashi *et al.,* 1998; Grimaldi *et al.,* 2009). As such, increased chloride concentrations of the magnitude we observed (>500%) almost certainly indicate some combination of increased evaporation and decreased inflow. Second, we found that concentrations of all six solutes were positively related to isotopically-derived E/I values. TN, in particular, had a strong relationship with E/I, even though it is subject to a far more complicated biogeochemistry than are semi-conservative ions. Lastly, climate records from the Yukon Flats largely agree with our observation that imbalanced E/I ratios are a primary driver of chemical changes in shrinking lakes. From 1980–2010 in the Yukon Flats, annual lake evaporation (46 cm) far exceeded annual precipitation (17–24 cm), while snowfall was 35% lower than during the prior 30 years of 1950–1980 (Jepsen *et al.,* 2013b). For lakes subject to shrinking, this combination of high evaporation and declining snowfall would act to concentrate nutrients and ions into smaller water volumes.

Permafrost degradation, commonly hypothesized as a mechanism behind shrinking lakes, may also contribute to observed changes in water chemistry. Namely, previously frozen

sediments become subjected to weathering and decomposition as they thaw, producing soluble materials that may runoff to nearby lakes (Kokelij *et al.,* 2009; Koch *et al.,* 2014). Nonetheless, we found that aquatic concentrations of TN and all four ions were unrelated to the probability of near-surface permafrost presence. This differs from many previous studies that documented higher concentrations of nitrogen and ions in aquatic systems located within discontinuous, unstable permafrost, owing to the increased rates of decomposition, weathering, and hydrologic export in such soils (Petrone *et al.,* 2006; Kokelij *et al.,* 2009; Harms & Jones 2012). However, permafrost degradation does not always increase solute concentrations in nearby waterbodies, especially when solutes are bioactive. Striegl et al. (2005) found decreased export of dissolved organic carbon to Subarctic rivers from 1978–1980 to 2001–2003, suggesting that increased flow path, residence time, and microbial mineralization rates within the soil active layer allowed much of the carbon to be respired before reaching rivers. Likewise, much of the nitrogen mobilized from thawing permafrost in our study area may be mineralized, denitrified, and released as gaseous nitrogen products within the soil active layer, thus having little impact on lake water chemistry. The apparent lack of connection between near-surface permafrost presence and water chemistry may also be due in part to the small catchments of our study lakes, and the extremely low landscape relief of the Yukon Flats (Lewis *et al.,* 2014). Small catchments restrict the terrestrial footprint from which lakes may receive permafrost-mediated solutes, while the flat landscape limits lateral fluxes of such solutes.

The lack of permafrost influence on water chemistry did not extend to phosphorus; TP concentrations of our study lakes were highest at intermediate values of permafrost presence, an unexpected result in view of our findings for TN and ions. The coarse resolution of TP, which does not distinguish between organic and inorganic forms, limits our ability to interpret why only

TP was related to permafrost presence. However, had the increased TP observed at intermediate permafrost levels been primarily recalcitrant organic matter, we would have expected a simultaneous increase in TN, which was not observed. This is because recalcitrant organic matter contains both nitrogen and phosphorus and, by resisting mineralization, moves the two nutrients through ecosystems in a coupled manner (Gibson & O'Reilly 2012). In contrast, inorganic phosphorus behaves uniquely in forest soils, especially in water-logged soils which are common in the Yukon Flats. Water saturation causes anoxic conditions, which in turn promotes release of inorganic phosphates via dissociation of the iron-phosphate complexes typical of aerated soils (Patrick & Khalid 1974). Thus, areas of intermediate permafrost cover may be experiencing greater increases in active layer depth, allowing water saturation to occur at deeper soil levels and thereby creating conditions conducive to hydrologic export of inorganic phosphates. Moreover, such processes may have become more pronounced in the most recent decade, as evidenced by the lack of change to TP concentrations in 5 shrinking lakes of the Yukon Flats as of 2001–2003 (Corcoran *et al.*, 2009).

Other processes not explicitly tested by our dataset may also have contributed to observed changes in water chemistry of shrinking lakes. As water levels recede, former benthic sediments become exposed, shifting from an anoxic to aerated state in the process. Aeration greatly accelerates decomposition in these newly exposed soils, creating a nutrient source that can be easily transported into lakes given the short distances involved (Koch *et al.*, 2014). The Yukon Flats has also experienced a substantial increase in fire activity in recent decades, and is considered one of the most flammable Subarctic regions in North America (Kasischke *et al.*, 2010; Kelly *et al.*, 2013). Fires release nutrients locked in terrestrial resources such as soils and vegetation, making them available for transport to lakes. In the 2 years following a fire at one of

our study sites, however, TN and TP concentrations remained unchanged, indicating no short-term impact of fires on lake water chemistry (Lewis *et al.,* 2014). Longer-term, fires may eventually impact lake water chemistry by removing the insulating ground cover that protects permafrost from thawing (O'Donnell *et al.,* 2011). Lastly, increased groundwater inputs may alter lake water chemistry due to its distinct solute composition that is rich in ions and dissolved inorganic matter and poor in dissolved organic matter (Walvoord & Striegl 2007). However, because our changes in water chemistry were limited to shrinking lakes, increased groundwater inflows seems an unlikely mechanism since it would presumably counteract lake drawdown. Additionally, for areas such as the Yukon Flats in which permafrost and fine-grained soils inhibit water infiltration, fluctuations in lake water levels are often driven by hydrological processes operating at or near the surface (Bouchard *et al.,* 2013).

Irrespective of the mechanism, the observed changes in water chemistry on shrinking lakes are substantial and likely to have significant ecological ramifications. In shallow lakes, nitrogen and phosphorus, rather than light or carbon, most typically limit productivity (Ogbebo *et al.,* 2009). Thus, the increased loads of nitrogen and phosphorus, combined with warmer water temperatures, may lead to an increase in total productivity of shrinking lakes. Increased productivity via eutrophication represents a potentially serious threat to lacustrine biodiversity, which generally declines as lakes shift to overly-productive states (Dodson *et al.,* 2000). Substantial nutrient increases have also been shown to cause shifts in stable states of shallow northern-latitude lakes, shifting from clear waters dominated by submersed aquatic vegetation to turbid, phytoplankton-dominated states (Bayley & Prather 2003). In lakes of the Yukon Flats, increased nitrogen levels caused earlier and more prolific phytoplankton blooms, thereby favoring zooplankton grazers over scraper and deposit-feeder invertebrates that are important to

nesting waterbirds (Corcoran *et al.,* 2009). These same nitrogen increases, however, did not cause elevated levels of chlorophyll-a in the water column (Corcoran *et al.,* 2009), suggesting that (*i*) Yukon Flats lakes are more commonly limited by phosphorus, and/or (*ii*) changes in lake productivity may be more evident via growth of macrophytes, which are abundant in these shallow lakes. Lastly, the ecological consequences of chemical changes in shrinking lakes are not restricted to nutrient enrichment, given the large concentration increases we observed for multiple ions. Increased ionic concentrations raise salinity, which in turn exerts strong controls on species occurrence. On shrinking lakes, elevated salinity may stress the normal lake biota up to some threshold, after which we see changes in species composition (Hart *et al.,* 2003).

The sizeable increases in nutrient and ion concentrations we observed for shrinking Subarctic lakes of the Yukon Flats are especially notable when considering the vast geographic extent from which shrinking lakes have been observed – from Siberia to Alaska to Canada – and the overall tendency for Arctic and Subarctic landscapes to contain numerous lakes. Moreover, these chemical changes are likely to persist, if not intensify, owing to continued climatic change at northern latitudes. In particular, warmer temperatures, longer ice-free seasons, and declining snowfall may further skew E/I ratios, which our data indicates to be a primary mechanism behind long-term changes in water chemistry of shrinking lakes. The high degree of solute enrichment we observed has been previously documented largely for ephemeral or semi-ephemeral lakes during their drawdown phase, but these effects are largely erased during semi-regular recharge events (Waiser 2006). In contrast, the shallow, closed-basin lakes of our Yukon Flats study area, and much of the Arctic and Subarctic overall, are generally not ephemeral, such that increased solute concentrations in shrinking lakes reflects an established trend that is unlikely to be reversed in the short-term.

3.6 Acknowledgements

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3.8 Figures

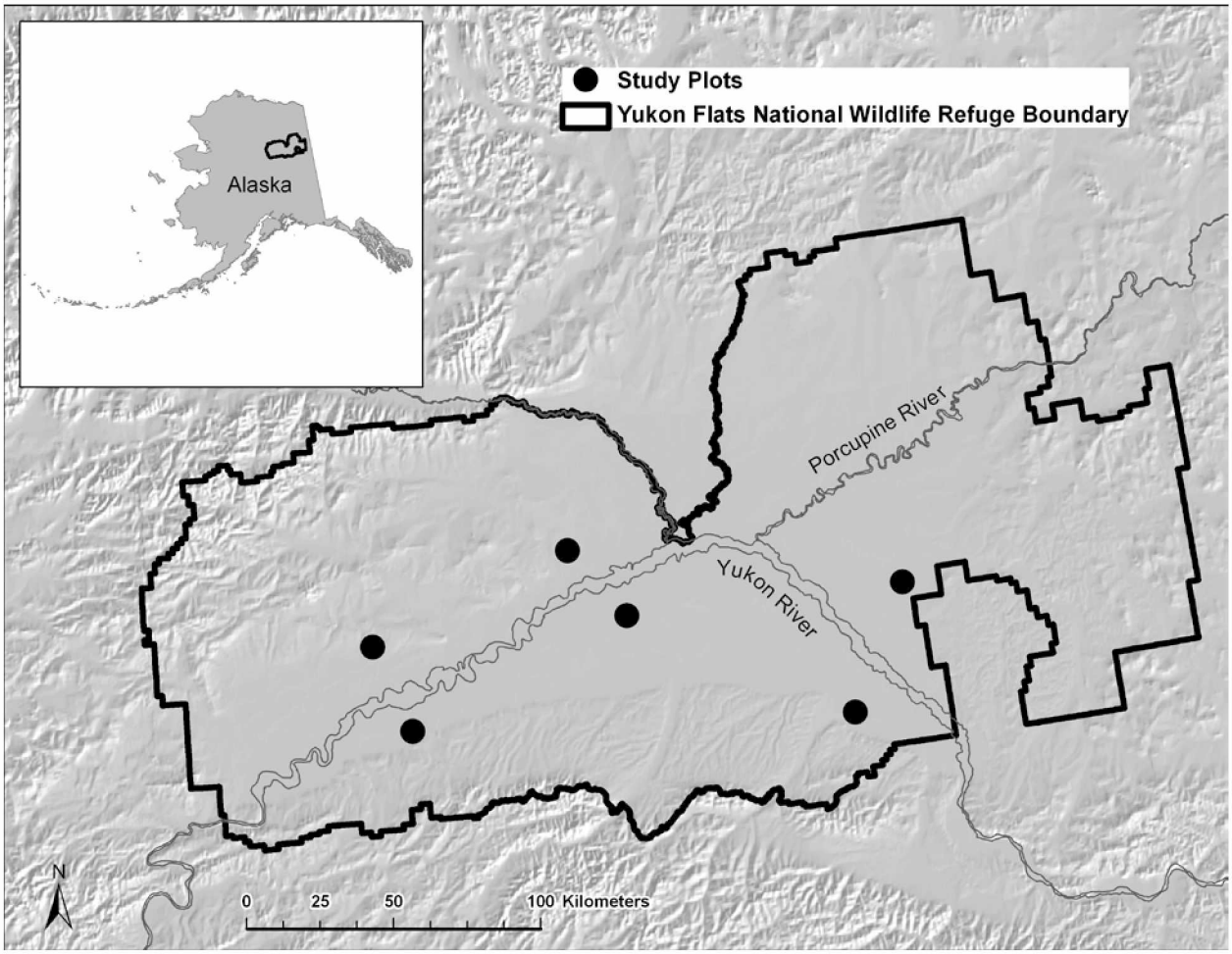

Figure 3-1. Map of the study area in the Yukon Flats National Wildlife Refuge, Alaska, showing the location of the 6 study plots.

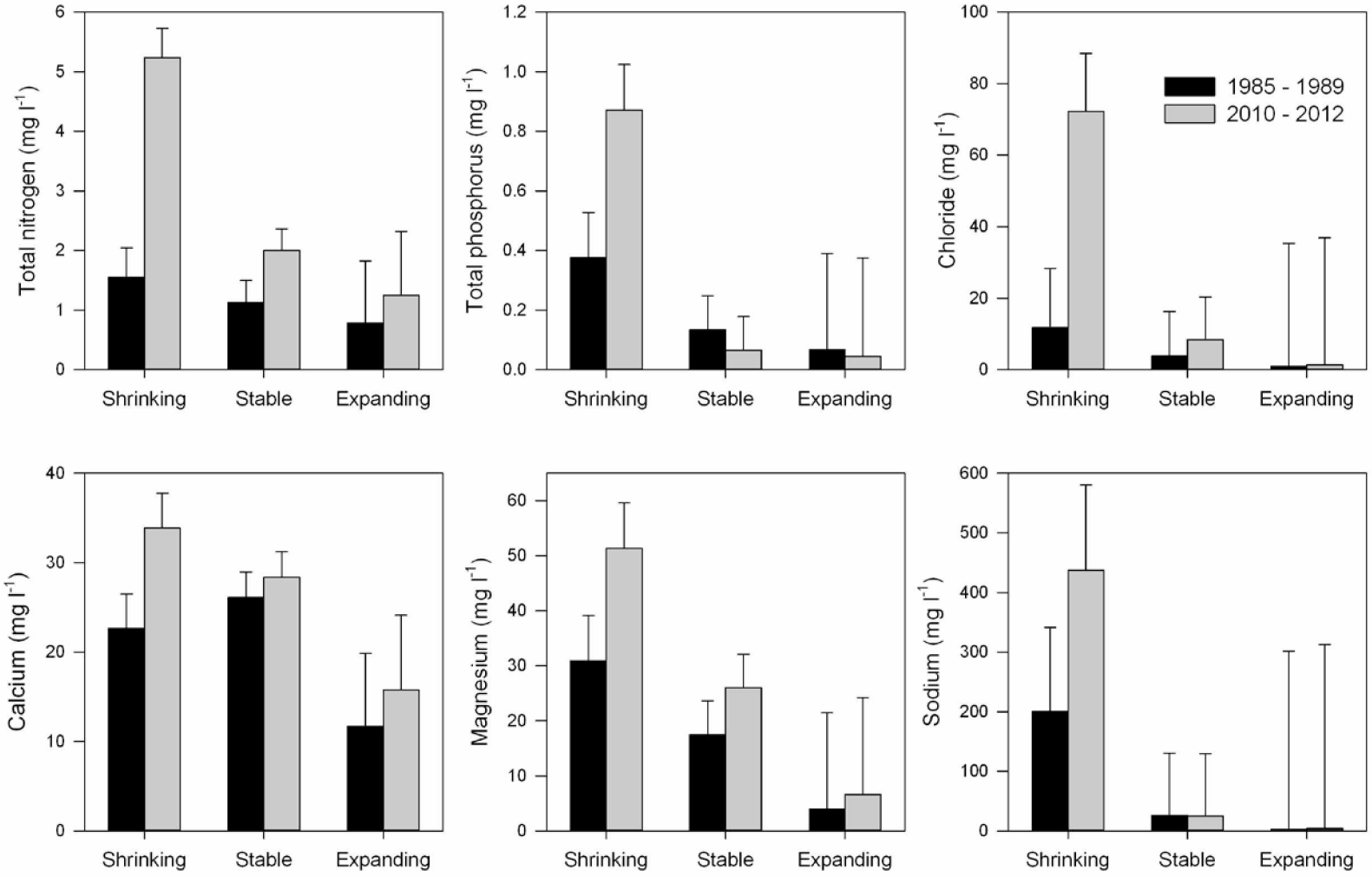

Figure 3-2. Aquatic concentrations of nutrients (total nitrogen, total phosphorus) and ions (calcium, chloride, magnesium, sodium) for shrinking, stable, and expanding Subarctic lakes of the Yukon Flats across two time periods: 1985–1989 versus 2010–2012. Data are restricted to lakes with surface areas > 1 ha (n = 55). Concentrations ± SE are based on parameter estimates from the best-fitting model, with all other model covariates held constant at their mean values.

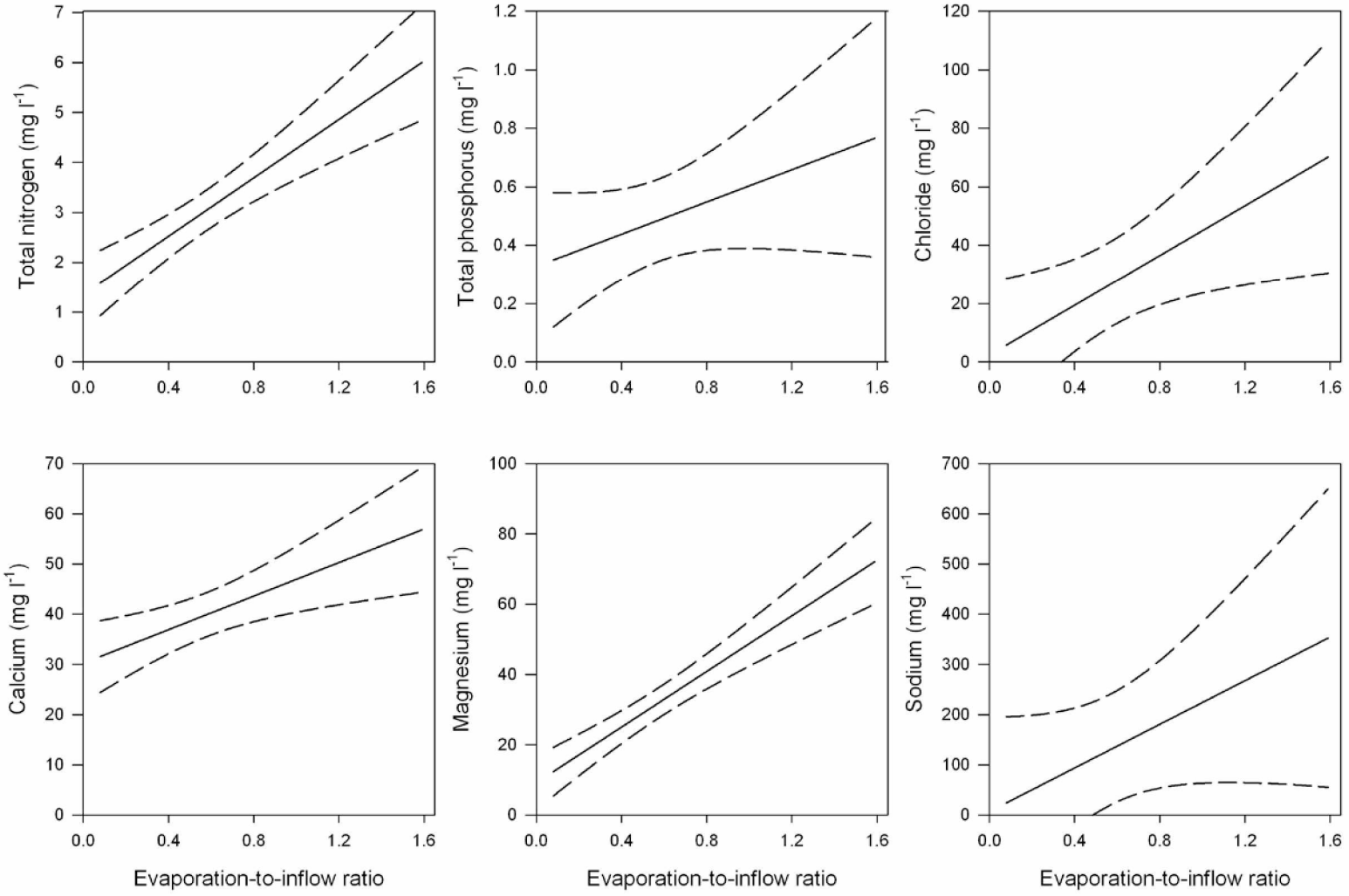

Figure 3-3. Aquatic concentrations of nutrients (total nitrogen, total phosphorus) and ions (calcium, chloride, magnesium, sodium) relative to evaporation-to-inflow ratio for Subarctic lakes (n = 74) of the Yukon Flats from 2010–2012. Concentrations are based on model-averaged parameter estimates, with all other model covariates held constant at their mean values. Dashed lines denote unconditional SEs.

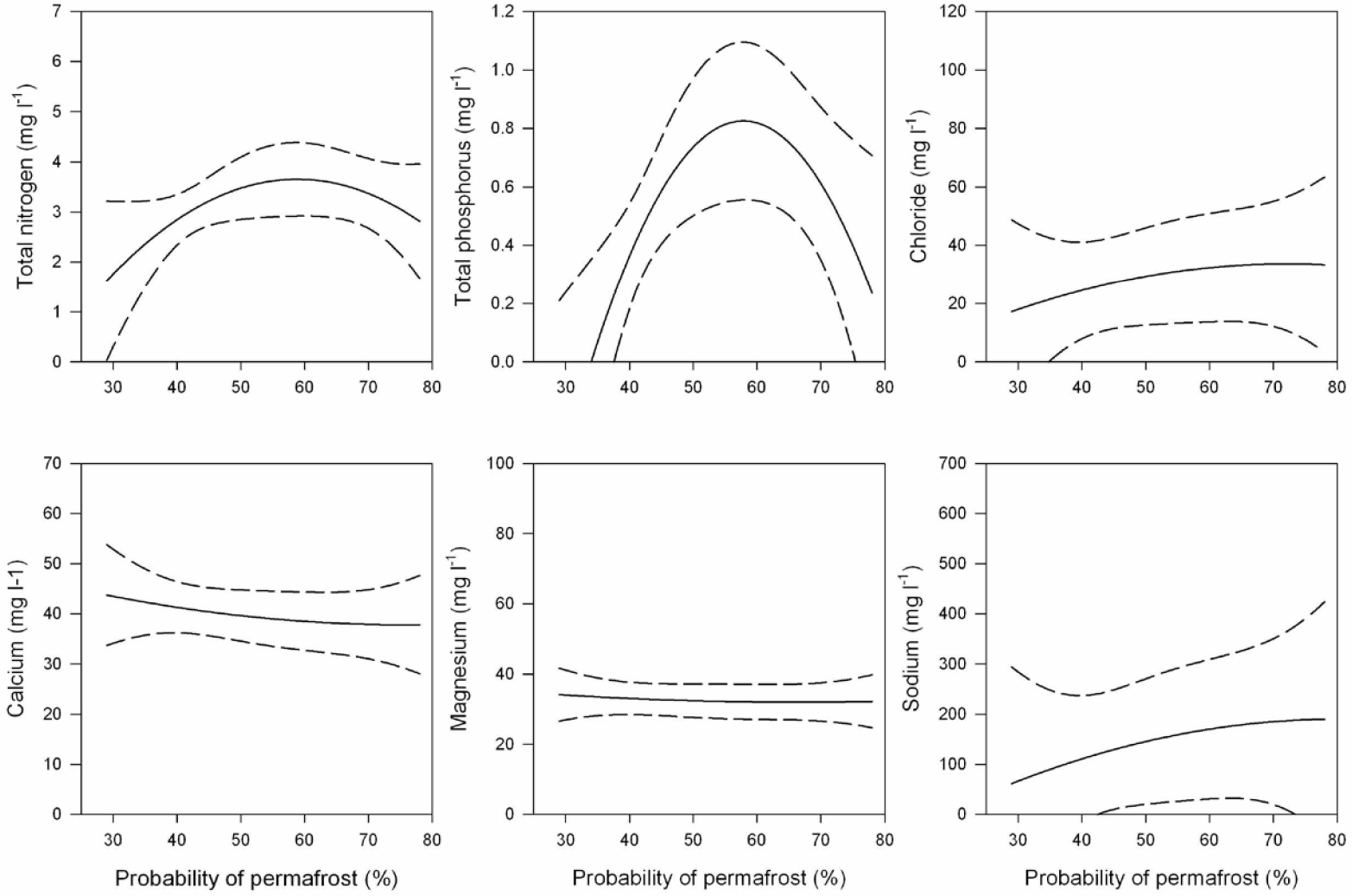

Figure 3-4. Aquatic concentrations of nutrients (total nitrogen, total phosphorus) and ions (calcium, chloride, magnesium, sodium) relative to probability (%) of permafrost presence for Subarctic lakes (n = 74) of the Yukon Flats from 2010–2012. Concentrations are based on model-averaged parameter estimates, with all other model covariates held constant at their mean values. Dashed lines denote unconditional SEs.

3.9 Tables

Table 3-1. Summary statistics describing physical characteristics of our study lakes (n = 74) in the Yukon Flats, Alaska. Shoreline development ratio relates the shoreline length of a lake to the circumference of a circle of equal area, where 1.0 is a perfect circle.

	Min.	Q1	Q3	Max.	Mean	SD
Lake area (ha)	0.03	1.19	13.55	283.18	15.77	37.74
Depth (m)	0.07	0.58	1.20	4.30	0.94	0.57
Shoreline development ratio	1.04	1.10	1.39	5.98	1.36	0.58

Table 3-2. Parameter estimates (Est) and standard errors (SE) from the best-fitting (ΔAIC = 0) linear mixed model describing variation in concentrations of two nutrients (total nitrogen, total phosphorus) and four ions (calcium, chloride, magnesium, and sodium) on shrinking, stable, and expanding Subarctic lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data presented in this table are restricted to lakes with surface areas > 1 ha (n = 55). Covariates include Ordinal (intra-annual date), Decade (1980s, 2010s), Extent (shrinking, stable, expanding), and a Decade*Extent interaction.

	Total nitrogen		Total phosphorus		Calcium		Chloride		Magnesium		Sodium	
Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Intercept	36.68	1179.95	-18.73	353.86	13.88	8.72	6.33	40.54	-12.97	17.91	-74.25	330.57
Ordinal	3.89	2.83	0.45	0.73	-0.01	0.02	-0.03	0.11	0.09	0.02	0.39	0.72
Decade	464.23	655.97	-22.27	172.06	4.09	3.64	0.36	25.50	2.66	4.21	3.81	170.18
Extent: Shrink	763.66	1153.01	308.66	357.55	10.96	9.07	10.79	38.32	26.93	19.43	200.12	331.48
Extent: Stable	344.00	1104.85	67.75	342.83	14.40	8.69	2.78	36.72	13.52	18.61	25.16	317.80
Decade*Extent: Shrink	3220.23	718.19	517.12	187.75	7.12	3.96	60.03	28.10	17.76	4.60	232.93	185.96
Decade*Extent: Stable	407.90	690.28	-46.89	180.93	-1.80	3.83	4.25	27.00	5.85	4.43	-4.77	178.98

Table 3-3. Model selection results from linear mixed models describing variation in concentrations of two nutrients (total nitrogen, total phosphorus) and four ions (calcium, chloride, magnesium, and sodium) on shrinking, stable, and expanding Subarctic lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Models are listed in order of ΔAIC and we also present number of parameters (k) and model weights (w_i). Data are restricted to lakes with surface areas > 1 ha (n = 55). Covariates include Ordinal (intra-annual date), Decade (1980s, 2010s), and Extent (shrinking, stable, expanding).

		Total nitrogen		Total phosphorus		Calcium		Chloride		Magnesium		Sodium	
Model	k	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i	ΔAIC	w_i
Ordinal + Decade + Extent + Decade*Extent	9	0	1	0	1	0	1	0	1	0	1	0	0.71
Ordinal + Decade + Extent	7	57.61	0	31.92	0	15.85	0	11.09	0	27.27	0	2.66	0.19
Ordinal + Extent	6	151.07	0	37.46	0	46.10	0	20.14	0	138.05	0	3.89	0.10
Ordinal + Decade	5	4561.90	0	4529.09	0	4073.61	0	2800.68	0	2233.79	0	4056.21	0
Null	3	4707.39	0	4553.55	0	4092.65	0	2809.88	0	2371.53	0	4055.56	0
Ordinal	4	4709.39	0	4554.78	0	4093.02	0	2811.65	0	2387.63	0	4057.39	0

Table 3-4. Model-averaged parameter estimates (Est) and unconditional standard errors (SE) from linear mixed models evaluating mechanisms driving variation in concentrations of two nutrients (total nitrogen, total phosphorus) and four ions (calcium, chloride, magnesium, and sodium) on Subarctic lakes (n = 74) of the Yukon Flats, Alaska, from 2010–2012. Covariates include Ordinal (intra-annual date), Year (2010, 2011, 2012), Area (lake surface area), Permafrost (probability of permafrost presence), Permafrost^2 (quadratic term), and E/I (evaporation-to-inflow ratio). Decimals are excluded for values >100.

	Total nitrogen		Total phosphorus		Calcium		Chloride		Magnesium		Sodium	
Covariate	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Intercept	-7877	8297	-4197	3221	38.04	45.22	-18.45	142.73	-9.99	33.60	-49.33	1043
Ordinal	12.42	3.63	0.24	1.14	-0.03	0.03	-0.02	0.15	0.13	0.02	-0.37	1.23
Year 2011	-202	230	31.92	72.48	10.61	1.72	-13.17	9.51	0.61	1.34	-118	77.95
Year 2012	-887	247	-75.96	77.78	9.05	1.85	-27.54	10.22	-2.44	1.45	-218	83.97
Area	-4.34	11.00	-1.16	3.86	-0.15	0.12	-0.14	0.39	0.10	0.12	-0.64	2.92
Permafrost	467	264	211	92	-1.54	2.95	5.26	9.45	-1.28	2.94	31.78	70.56
Permafrost^2	-3.97	2.47	-1.83	0.87	-0.04	0.06	-0.04	0.09	0.01	0.03	-0.20	0.66
E/I	2911	1056	272	372	16.76	11.43	42.41	36.03	39.63	11.00	215	269

Reference values for categorical parameters: Year – 2010.

Table 3-5. Model selection results, listed in order of ΔAIC, from linear mixed models evaluating mechanisms driving variation in concentrations of two nutrients (total nitrogen, total phosphorus) and four ions (calcium, chloride, magnesium, and sodium) on Subarctic lakes (n = 74) of the Yukon Flats, Alaska, from 2010–2012. Results are restricted to well-supported models (ΔAIC $\leq$ 2) and the null intercept-only model, and we also report number of parameters (k) and model weights (w_i). Covariates include Ordinal (intra-annual date), Year (2010, 2011, 2012), Area (lake surface area), Permafrost (probability of permafrost presence), and E/I (evaporation-to-inflow ratio).

Covariate	Model	k	ΔAIC	w_i
Total nitrogen	Ordinal + Year + Permafrost + EI	9	0	0.41
	Ordinal + Year + EI	7	0.58	0.31
	Ordinal + Year + Permafrost + Area + EI	10	1.81	0.17
	Null	3	112.81	0
Total phosphorus	Ordinal + Year + Permafrost + EI	9	0	0.57
	Ordinal + Year + Permafrost + Area + EI	10	1.90	0.22
	Null	3	73.93	0
Calcium	Ordinal + Year + EI	7	0	0.41
	Ordinal + Year + Area + EI	8	0.46	0.33
	Null	3	75.26	0
Chloride	Ordinal + Year + EI	7	0	0.55
	Ordinal + Year + Area + EI	8	1.89	0.21
	Null	3	56.25	0
Magnesium	Ordinal + Year + EI	7	0	0.56
	Ordinal + Year + Area + EI	8	1.38	0.28
	Null	3	83.69	0
Sodium	Ordinal + Year + EI	7	0	0.55
	Ordinal + Year + Area + EI	8	1.96	0.21
	Null	3	76.06	0

Chapter 4

Cross-trophic resilience of shrinking Subarctic lakes to rising nutrient and ion concentrations: from primary producers to top predators[3]

4.1 Abstract

Climate-driven losses in lake surface area have been observed for several Arctic and Subarctic regions in recent decades. These losses in lake area, by concentrating solutes into smaller water volumes, may cause pronounced changes in water chemistry, with potentially significant consequences for lake ecosystems. In particular, elevated nutrient concentrations may increase primary productivity, which may then transfer upward to higher trophic levels. Moreover, higher ion concentrations may exceed physiologic thresholds of aquatic organisms with low salt tolerance. We examined ecosystem changes on shrinking versus stable lakes of the Yukon Flats, Alaska, from 1985–1989 to 2010–2012, focusing on changes to abundance and distributions of organisms from 3 successive trophic levels: phytoplankton, aquatic invertebrates, and waterbirds. Specifically, we sampled 18 shrinking lakes that had experienced pronounced increases in nutrient (>200% for total nitrogen, >100% for total phosphorus) and ion concentrations (>100% for 4 major ions combined) from 1985–1989 to 2010–2012, versus 37 stable lakes with relatively little chemical change over the same time period. At the base of the food web, we found that phytoplankton stocks, as indexed by chlorophyll concentrations, remained largely unchanged on both shrinking and stable lakes from the 1980s to 2010s. Moving up the trophic chain, we found large changes in invertebrate abundance across decades, including decreased abundance of 5 of the 6 groups we examined. However, these decadal changes were not limited to shrinking lakes,

[3] Prepared for submission to Oecologia as Lewis, T.L., P.J. Heglund, M.S. Lindberg, J.A. Schmutz, J.H. Schmidt, A.J. Dubour, J. Rober, and M.R. Bertram. 2015. Cross-trophic resilience of shrinking Subarctic lakes to rising nutrient and ion concentrations: from primary producers to top predators.

occurring on lakes with stable surface areas as well. Finally, at the top of the food web, we observed that occupancy rates of 10 waterbird species, including adults and chicks, remained unchanged from 1985–1989 to 2010–2012. In summary, while decadal changes to lake ecosystems were observed, most notably for aquatic invertebrates, these changes were not exclusive to shrinking lakes, occurring on lakes with stable surface areas as well. This suggests that, to date, ecosystems of shrinking lakes in the Yukon Flats were largely resilient to rising chemical concentrations, as increased nutrient and ion loads did not propagate across 3 broad trophic levels.

4.2 Introduction

The highest total global concentration of lakes occurs at Arctic and Subarctic latitudes (Verpoorter et al. 2014). These waterbodies provide important habitat for a diversity of wildlife species, especially migratory waterbirds that breed there in the tens of millions. The region's vast lakes are largely a byproduct of its cold climate, in which short ice-free seasons limit evapotranspiration and widespread permafrost inhibits soil permeability (Ford and Bedford 1987). In recent decades, however, Arctic and Subarctic regions have experienced a period of unprecedented warming (Callaghan et al. 2004, New et al. 2011), potentially stressing the long-term water balance of northern lakes and ponds. In particular, warmer temperatures may lead to longer ice-free seasons and increased evaporative water loss (Magnuson et al. 2000, Smol and Douglas 2007), while simultaneously increasing drainage of lake water via degradation of extant permafrost (Jorgenson et al. 2001, Jepsen et al. 2013a). To date, net losses in lake surface area have been documented for Arctic and Subarctic regions of Alaska (Riordan et al. 2006, Rover et al. 2012), Canada (Smol and Douglas 2007, Carroll et al. 2011), and Siberia (Smith et al. 2005).

Two of the major processes likely responsible for losses in lake surface area – increased evaporation and permafrost thaw – may also cause pronounced changes in water chemistry of shrinking lakes (Lewis et al. 2015a). Increased evaporation, if not balanced by concurrent increases to water inputs, concentrates solutes into smaller water volumes. Lakes that lose water in this manner tend to exhibit greater increases in nutrient and ion concentrations than those that lose water via surface outflow or subsurface infiltration (Fritz 1996, Koch et al. 2014). Likewise, thawing permafrost exposes previously frozen organic matter to decomposition and mineralization, releasing nutrients and other solutes that may be flushed from soils to lakes (Petrone et al. 2006, Wrona et al. 2006). Overall, recent research has indicated that shrinking lakes, relative to their stable counterparts, have higher specific conductivities (Roach et al. 2011), indicative of higher ion loads, and higher nitrogen and phosphorus concentrations (Corcoran et al. 2009, Lewis et al. 2015a).

Despite these compelling trends on shrinking lakes, little is known of how such chemical changes may propagate through lake ecosystems, including potential ramifications for lacustrine wildlife. In general, nitrogen and phosphorus, rather than light or carbon, most typically limit productivity in shallow Arctic and Subarctic lakes (Ogbebo et al. 2009). Accordingly, as nitrogen and phosphorus concentrations increase, shrinking lakes may experience elevated productivity, in which the added nutrients stimulate primary production and thereby add more overall energy to the lake ecosystem (Waide et al. 1999, Dodson et al. 2000). Increased primary productivity at the base of the food web may, in turn, transfer upward to primary consumers, thereby driving increases in their overall abundance and biomass (Peterson et al. 1993, Slavik et al. 2004). In Arctic and Subarctic lakes, primary consumer communities are typically dominated by aquatic invertebrates, whose populations may quickly track changes in primary productivity because of

their low generation times and high fecundity (Feuchtmayr et al. 2010, Greig et al. 2012). For example, experimental fertilization of a shallow Arctic lake caused increased benthic and planktonic primary production, which in turn supported a three- to five-fold increase in snail densities (Hershey 1992, Hobbie et al. 1999). However, chironomid densities in this same Arctic lake were unaffected by nutrient additions, exemplifying that the response of invertebrates to fertilization varies widely by taxa. In addition to nutrients, abundance of aquatic invertebrates may also vary in response to salinity, although responses are based more on physiology than on trophic energy flow (Pinder et al. 2005). As ions concentrate in shrinking lakes (Lewis et al. 2015a), raising salinity levels, aquatic invertebrates with low salt tolerances may become osmotically stressed, causing reduced growth or death (James et al. 2003). Hence, simultaneous increases of nutrients and ions in shrinking lakes may have opposing effects on invertebrate abundance, favoring some taxa while harming others.

Aquatic invertebrates constitute the primary prey base for a variety of predators in Arctic and Subarctic lakes, including fish and waterbirds (Lewis et al. 2015b). Accordingly, changes in invertebrate abundance may transfer upward to the highest trophic levels, thereby influencing distributions and abundance of several animals that hold significant anthropogenic and economic value. In this manner, rising nutrient concentrations in shrinking lakes may ultimately cascade across multiple trophic levels, from primary producers to aquatic invertebrates to predators (Carpenter et al. 1985). Such cross-trophic cascades have been experimentally demonstrated in freshwater systems through the use of artificial fertilization; long-term additions of phosphorus to an Arctic stream caused a positive response at all trophic levels, including increases in algal stocks, grazing invertebrate densities, and fish growth rates (Slavik et al. 2004). In addition to trophic cascades, pronounced changes in salinity may directly impact certain freshwater

predators, such as fishes, by causing osmotic stress, while having little impact on waterbirds and other semi-aquatic species (James et al. 2003).

Our study was situated on the Yukon Flats, a large boreal basin in Subarctic Alaska, where high evaporation rates (Anderson et al. 2013), decreased snowfall (Jepsen et al. 2013b), and thawing permafrost (Jepsen et al. 2013a) have contributed to net losses in lake surface area in recent decades. Of more than 15,000 lakes examined in the region, approximately 9-16% decreased in surface area extent from 1979 to 2009 (Rover et al. 2012). These losses in lake surface area caused substantial changes in water chemistry; of 55 lakes originally sampled for water chemistry during 1985–1989, 18 shrank over the intervening 25 years, leading to solute concentrations that had, by 2010–2012, increased by >200% for total nitrogen, >100% for total phosphorus, >40% for calcium, >500% for chloride, >50% for magnesium, and >100% for sodium (Lewis et al. 2015a). Conversely, of the remaining 37 lakes with stable (n = 33) or expanding (n = 4) surface areas, nutrient and ion concentrations remained relatively unchanged. These same 55 lakes were simultaneously sampled for abundance of common autotrophic and heterotrophic organisms, providing us a unique opportunity to examine impacts of chemical changes on food webs of shrinking lakes. Specifically, we examined food webs in shrinking versus stable lakes of the Yukon Flats from 1985–1989 to 2010–2012, focusing on three broad trophic levels: (1) phytoplankton, indexed by chlorophyll concentration, (2) aquatic invertebrates, and (3) waterbirds, which served as top predators in the absence of fish. Moreover, our study design, though non-manipulative, offered a before-after-control-impact (BACI) framework, with control (stable lakes) and experimental (shrinking lakes) units measured both pre- (1985–1989) and post-impact (2010–2012). BACI designs, which are rarely available for naturally occurring impacts such as ours, avoid the primary pitfall of many environmental

disturbance studies, in which differences between experimental and control sites may be unrelated to the disturbance, having existed beforehand.

Overall, the goals of our study were two-fold, assuming aspects of both exploratory and confirmatory research: (1) Exploratory - we provide an initial examination of how ecosystems of Arctic and Subarctic lakes responded to enduring losses in surface area, thereby gaining novel insights that inform future research and conservation efforts. (2) Confirmatory – using a bottom-up trophic framework, we predicted that increased nutrient concentrations in shrinking lakes would stimulate phytoplankton production, which would subsequently support increased abundance of aquatic invertebrates, including primary and secondary consumers. More abundant invertebrate populations would subsequently influence waterbird distributions, evident via increased waterbird occupancy rates on shrinking lakes.

4.3 Materials and Methods

Study Area

The Yukon Flats is a large basin in interior Alaska bisected by the Yukon River and encompassed by the 34,800 km^2 Yukon Flats National Wildlife Refuge. The refuge contains more than 40,000 lakes and wetlands and is largely pristine natural habitat, with no road infrastructure and around 1,000 permanent inhabitants. The area experiences a continental Subarctic climate, characterized by low precipitation and seasonal daylight and temperature extremes. Annual precipitation is 17 cm and summer and winter temperatures average 15 and -27 °C, respectively (National Climate Data Center). The area is underlain by continuous and discontinuous permafrost (Pastick et al. 2013) and generally has low landscape relief (<50 m). Mixed boreal forest covers much of the Yukon Flats and is dominated by black (*Picea mariana*)

and white spruce (*P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.).

Our research was conducted on 6 randomly selected study plots located throughout the Yukon Flats National Wildlife Refuge (Fig. 1). These plots, which were originally used for limnological and avian research during the 1980s (Heglund and Jones 2003), measured 10.36 km^2 and contained from 7–17 lakes, for a total of 77 study lakes. Lakes varied in size from <1 ha to >200 ha, but were uniformly shallow, rarely measuring deeper than 2 m. Lake basins were largely closed, with few well-defined inlet or outlets. This combination of shallow depth and lack of surface outlets precluded permanent fish in all our study lakes, and no fish were observed during our study.

Chlorophyll

During 1985–1989, chlorophyll concentration of each lake was sampled 1–2 times per month (June–Sept) in 2 of 5 years, with the exception of 15 lakes sampled in ≥3 years. We re-sampled these same lakes for chlorophyll concentration from 2010–2012, sampling each lake once per month (Jun–Aug) in 2 of 3 years, with the exception of 17 lakes sampled in all 3 years. Our chlorophyll samples, which represent water column chlorophyll levels, were collected using identical field methodologies in each decade. First, we collected 8 l of water from near the lake's midpoint and 25 cm below the surface. We then filtered measured volumes of lake water on site through Gelman A/E glass fiber filters (Gelman Filters, Pall Corporation, Port Washington, New York, USA) until a visually noticeable algal stain developed on the filter, collecting 2 filters per sample event. Following their use, filters were immediately placed in protective sleeves, desiccated with silica gel beads, and kept in dark, cool storage until transported to freezers. In the

laboratory, chlorophyll was extracted with 90% ethanol and concentrations were determined with fluorometric methods (Knowlton 1984). This extraction method was replicated for each decadal period (1985–1989 and 2010–2012), including use of the same laboratory (Jones Limnology Lab, University of Missouri, Columbia, Missouri, USA). Our final chlorophyll values were averaged from the two filters collected per sample event and were corrected for the volume of water passed through each filter.

Aquatic Invertebrates

Our study lakes were initially sampled for aquatic invertebrate abundance from 1985–1989. Because intra-annual sample dates from this period were missing, we were unable to assess number of sample events per lake per month; however, the majority of lakes were sampled in 2 of 5 years from 1985–1989, thus including sources of inter-annual variation. We re-sampled these same lakes for aquatic invertebrates from 2010–2012, sampling each lake once per month (Jun–Jul) in 2 of 3 years, with the exception of 17 lakes sampled in all 3 years. We replicated our methods for sampling aquatic invertebrates, described below, from 1985–1989 to 2010–2012. We collected aquatic invertebrates along transects located at random locations along lake perimeters and oriented perpendicular to shore. We scaled number of transects to lake area, with a minimum of 2 and maximum of 21 transects per lake. The number of transects per lake and their general locations were approximately replicated across decades. Along each transect we collected 1 invertebrate sample per vegetative zone, and a typical transect contained 2 samples. Vegetative zones included emergent and submergent vegetation, with the most common plants being cattail (*Typha latifolia*), pondweed (*Potamageton* spp.), sedge (*Carex* spp.), and hornwort (*Ceratophyllum demersum*). In the event that we encountered ≤1 vegetative zone, we collected

an extra sample in the open water zone. We used a D-frame sweep net (0.5-mm mesh) to collect invertebrates from the water column, pulling it horizontally for 1 m just below the water surface and through the vegetation. We placed invertebrates in ethanol and transported samples to the laboratory, where we identified invertebrates to minimal taxonomic groupings, typically family, and enumerated number of individuals per group.

Waterbirds

During 1985–1989, each lake was surveyed for waterbirds 1–3 times per month in 2 of 5 years, with the exception of 18 lakes that were surveyed in 4 years. We re-surveyed these same lakes from 2010–2012, surveying each lake 1-2 times per month (Jun-Aug) in 2 of 3 years (2010-2012), with the exception of 17 lakes that we surveyed in all 3 years. We timed our surveys to cover the breeding cycle, from nesting (early Jun) through brood-rearing (Jul–Aug). We conducted waterbird surveys from shore on small lakes and from canoes on large lakes. We recorded species, sex, and age (adult vs. chick) of each individual observed on the lake. Our survey methods were approximately replicated across decades, with the exception that our 2010–2012 surveys consisted of 2 independent counts conducted over a 1–2 day period to allow for estimation of detection probability (see *Analyses* below; MacKenzie et al. 2002). See Lewis et al. (2015b) for a complete description of our repeat survey methods used for detection estimation.

Lake Surface Area

We used linear trends in lake surface area from 1979–2011, following methods described in Rover et al. (2012), to categorize each of our study lakes as shrinking (>20% decrease) or stable (<20% decrease). Linear trends are lake-specific slope values derived from regression models

that used time as the predictor variable and surface area as the response variable. We derived lake surface areas across the 32 year period from Landsat data with a supervised decision tree classification model to differentiate water from terrestrial surfaces. We selected Landsat data for 22 unique acquisition dates that provided minimal cloud obstruction across a wide geographic area. These 22 dates covered 16 of the 32 years and the bulk of the ice-free season (8 May to 16 Sept), thus including sources of both intra- and inter-annual variation. We used a conservative cut-off of >20% loss in surface area to classify lakes as shrinking, rather than a continuous description, to account for the coarse resolution (30 m pixel) of Landsat imagery and the high-degree of inter-annual variation in surface area. Further, we restricted this classification to lakes with a surface area >1 ha (n = 55) because lakes smaller than this size could not be reliably classified using Landsat imagery.

Analyses: chlorophyll and aquatic invertebrates

Our first analysis examined changes in chlorophyll levels from 1985–89 to 2010–12 on shrinking versus stable lakes. We used chlorophyll concentration (µg/l) as our response variable for a series of general linear mixed models, with our model set consisting of 5 *a priori* models: a null intercept-only model; a model with ordinal date (intra-annual date on a scale of 1-366) and decade (defined categorically as 1980s vs. 2010s); a model with ordinal date and extent (defined categorically as shrinking vs. stable); a model with ordinal date, decade, and extent; and a model with ordinal date and an interaction between decade and extent. The interaction model, in particular, provides important insight into long-term impacts of chemical changes on shrinking lakes; under a BACI study design, a significant effect of the ecological impact appears via the interaction between site (stable vs. shrinking lake) and time (1985–1989 vs. 2010–2012). We

included ordinal date in every model, with the exception of the null model, to control for intra-annual differences in chlorophyll levels, which was not our primary interest, but could confound our interpretation. We also included lake identity as a random effect in all models. This analysis was restricted to lakes with a surface area >1 ha (n = 55), from which we analyzed 869 chlorophyll samples collected across the two decadal periods.

For our second analysis, we examined changes in abundance of aquatic invertebrates from 1985–89 to 2010–12 on shrinking versus stable lakes. We narrowed our examination of aquatic invertebrates to 6 taxonomic groups that were both abundant and important prey of waterbirds: Amphipoda, Chironomidae, Coleoptera, Corixidae, Gastropoda, and Odonata. These 6 taxonomic groups together accounted for 65% of total invertebrates in our samples. For each taxonomic group we fit a series of generalized linear mixed models to explore changes in invertebrate abundance from 1985–89 to 2010–12, using raw invertebrate counts (individuals per sample) as our response variable. Such count data are usually fit with Poisson distribution models; however, our variance was degrees of magnitude larger than the mean, suggesting Poisson models were not appropriate for our data. Hence, we fit our most parameterized model with Poisson, negative binomial, and zero-inflated Poisson and negative binomial distributions, and then compared model fit with Akaike's Information Criterion (AIC). Our model selection indicated that a negative binomial provided the best fit for our count data, and all further models were fit using negative binomial generalized linear mixed models. Our model set was identical to that used for our chlorophyll analysis, with the exception that ordinal date, being unavailable for our 1980s data, was not included in any model. Likewise, we included lake identity as a random effect in all models and restricted this analysis to lakes with a surface area >1 ha (n = 55). Our analysis consisted of 4881 invertebrate samples with a combined count of 336,178 individuals.

Our chlorophyll models were run using the 'nlme' package (Pinheiro et al. 2013) and our invertebrate models the 'lme4' package (Bates et al. 2014) in program R. We used an information-theoretic approach to model selection for our chlorophyll and invertebrate models (Burnham and Anderson 2002), in which we compared the relative fit of models within a candidate set using AIC and AIC weights (w_i). We based inference of fixed effects on model selection metrics (ΔAIC, w_i) and precision of parameter estimates. When 95% confidence intervals overlapped 0.0, the parameter was deemed uninformative. We used parameter estimates and standard errors (SEs) from the highest-ranked model when a clear top model emerged. Otherwise, when model sets displayed selection uncertainty, we used model-averaged parameter estimates and unconditional SEs (Burnham and Anderson 2002).

Analyses: waterbirds

We examined decadal changes in distributions of waterbirds on lakes of the Yukon Flats by fitting a hierarchical Bayes' single-season occupancy model to our waterbirds survey data (MacKenzie et al. 2002). These models simultaneously estimated probability of lake occupancy by waterbirds (ψ) and probability that a waterbird was detected given presence (p). Such models were appropriate for our data because of the low detection probabilities observed for many waterbird species, especially during the breeding season when broods and hens are highly secretive (Walker et al. 2013, Lewis et al. 2015b). We converted counts of each species per lake per survey to presence or non-presence; a species was considered present if $\geq$1 individual was detected.

Occupancy models require temporally replicated presence/absence data in order to simultaneously estimate ψ and p (MacKenzie et al. 2002). To accommodate this data structure,

surveys are typically designed in a nested fashion whereby a primary survey consists of $k \geq 2$ secondary surveys. Moreover, occupancy models assume that the occurrence state of a site does not change over the duration of a primary survey. For waterbirds, which are highly mobile, this assumption is typically met by conducting all secondary surveys either simultaneously, or within a narrow time frame (e.g., <24 hrs). Our waterbird surveys conducted during the 1980s, however, did not incorporate temporally replicated secondary surveys (i.e., $k = 1$). Rather, while we surveyed each lake multiple times per year in the 1980s, days to weeks elapsed between each survey. Accordingly, to create the nested data structure needed for occupancy models, we treated each survey per lake per year as a secondary survey, with the whole of these secondary surveys combining to create the primary survey unit. Thus, each primary survey used in our occupancy models contained 1 year's worth of survey data per lake. This data design violates the closure assumption because waterbirds may have emigrated from a lake during our primary survey unit. However, violation of this assumption is not always that problematic (Kery and Schaub 2011), because temporary absence of a species from a site will be incorporated as one component of imperfect detection. Consequently, for our study, ψ is defined as the proportion of lakes occupied at least once during the decadal study period, rather than the proportion of lakes that were permanently occupied, as would be the case had the closure assumption been met (Mordecai et al. 2011, Kery and Schaub 2011).

Our 2010–2012 survey design differed from that of the 1980s in that each waterbird survey consisted of $k = 2$ secondary surveys, each being completed within a 24 hour window (Lewis et al. 2015b). Accordingly, to create consistency between our decadal datasets for occupancy modeling, we combined each of these original secondary surveys from 2010–2012 into one presence/absence record (i.e., $k = 1$). For example, a positive detection during secondary

survey 1 and non-detection during secondary survey 2 were treated as a single 'presence' in our updated data structure. This is because the species, although undetected during secondary survey 2, was indeed present on the lake. Next, we treated our original primary surveys from 2010–2012 as secondary surveys, thereby matching the data structure of our 1980s database in which secondary survey units are temporally separated by days to weeks. Under this updated data structure, we conducted 189 primary surveys that contained, on average, $k = 3.66$ secondary surveys during 1985–1989, versus 169 primary surveys containing an average of $k = 3.45$ secondary surveys during 2010–2012.

We fit one occupancy model for each of the 10 most common waterbird species observed during our surveys, which together accounted for >95% of total individuals counted: American Wigeon (*Anas Americana*), Canvasback (*Aythya valisineria*), Green-winged Teal (*Anas crecca*), Horned Grebe (*Podiceps auritus*), Mallard (*Anas platyrhynchos*), Northern Pintail (*Anas acuta*), Northern Shoveler (*Anas clypeata*), Ring-necked Duck (*Aythya collaris*), Lesser Scaup (*Aythya affinis*), and White-winged Scoter (*Melanitta fusca*). We also fit separate models for adults and ducklings of each species, for a total of 20 occupancy models (i.e., 10 species x 2 age groups). We modeled p in relation to 2 covariates that may affect detection: ordinal, which controlled for time-dependent changes in size and behavior of waterbirds and their chicks, and decade (1980s vs. 2010s), which accounted for decadal differences in survey design explained above. We modeled ψ in relation to 1 covariate, decade, to assess changes in distributions of waterbirds from 1985–1989 to 2010–2012. We did not include extent (stable vs. shrinking lake) as a covariate because our occupancy models generally failed to converge upon parsing of our survey data into 4 categories (i.e., 1980s shrinking, 1980s stable, 2010s shrinking, 2010s stable). Moreover, this allowed us to include data from 22 lakes that were too small (<1 ha) for accurate

lake extent categorization, raising our samples size for occupancy models from 55 to 77 lakes. Finally, we modeled p and ψ using the logit-link function and included lake identity as a random effect in all our occupancy models.

We performed Bayesian analysis of occupancy models using R2WinBUGS in program R (Sturtz et al. 2005), which called on WinBUGS version 1.4 (Lunn et al. 2000) to run a Markov chain Monte Carlo algorithm. We used an uninformative normal prior with a logit-scale mean of 0.0 and standard deviation of 0.01. We normalized continuous covariates to a mean of 0.0 and assessed convergence using the R-hat statistic (Gelman and Hill 2007). We based our inference regarding effect sizes of covariates on posterior means and 95% Bayesian credible intervals (BCI). When 95% BCI overlapped 0.0, we deemed the covariate uninformative. Likewise, for each waterbird species, we deemed broadly overlapping 95% BCI across decades to indicate a lack of difference in ψ from 1985–1989 to 2010–2012.

4.4 Results

Chlorophyll

Of the 55 study lakes with a surface area >1 ha, 18 were classified as shrinking and 37 as stable. Viewed across decades, these losses in lake surface area had no discernible impact on chlorophyll concentrations of Yukon Flats lakes. Chlorophyll levels on both stable and shrinking lakes remained relatively unchanged from 1985–1989 to 2010–2012 (Fig. 2). The decade*extent interaction, which tested for different decadal changes in chlorophyll levels on stable versus shrinking lakes, received low model selection support (w_i = 0.17; Table 1) and had a parameter estimate with 95% CI that broadly overlapped zero (β = -5.41 ± 9.11; Table 2). The best-fitting model (w_i = 0.59) to explain variation in chlorophyll concentration contained ordinal date and

extent as covariates (Table 1), indicating that chlorophyll levels were nominally higher on shrinking versus stable lakes. However, the parameter estimate for extent was poorly estimated ($\beta = -4.54 \pm 6.44$; Table 2) and there was considerable overlap of 95% CI between stable and shrinking lakes (Fig. 2). Finally, the model with decade and extent received moderate support ($w_i = 0.24$), but both covariates (decade: $\beta = 2.50 \pm 6.80$) had 95% CI that widely overlapped zero (Table 2).

Aquatic Invertebrates

All 6 invertebrate groups experienced considerable changes in abundance from 1985–1989 to 2010–2012. Specifically, abundance of 5 invertebrate groups - Amphipoda, Coleoptera, Corixidae, Gastropoda, and Odonata - decreased from 1985–1989 to 2010–2012, while that of Chironimidae increased over the same period. However, with the exception of Amphipoda and Corixadae, these decadal changes in abundance were largely independent of losses in lake surface area, having a similar magnitude and direction of change on both shrinking and stable lakes (Fig. 3). For Gastropoda and Odonata, comparable decadal changes in abundance on shrinking and stable lakes were evident via strong support for the decade covariate, combined with lack of support for decade*extent (Table 3). The best-supported model describing variation in abundance of Gastropoda ($w_i = 0.55$) and Odonata ($w_i = 0.63$) contained the covariate of decade (Table 3), with predicted values from this model indicating that abundance of Gastropoda and Odonata decreased by 78% and 50% from the 1980s to 2010s, respectively. In contrast, the decade*extent interaction received low model support and had 95% CI that widely overlapped zero for both Gastropoda ($w_i = 0.24$; $\beta = -0.26 \pm 0.37$) and Odonata ($w_i = 0.12$; $\beta = 0.12 \pm 0.41$). For Coleoptera and Chironomidae, the best-supported model contained decade*extent (Table 3),

suggesting differential decadal changes in abundance on shrinking and stable lakes. However, decade*extent was poorly estimated with 95% CI that overlapped 0 for both Coleoptera (β = -0.42 ± 0.43) and Chironomidae (β = 0.31 ± 0.51; Table 4). Predicted model values indicate that abundance of Coleoptera decreased by 74% from the 1980s to 2010s, while that of Chironomidae increased by 194% over this same period. Overall, of all covariates considered, the decade covariate had the largest effect size and most precise estimate for each of the 6 invertebrate groups (Table 4).

For Amphipoda and Corixidae, magnitude of changes in abundance from 1985–1989 to 2010–2012 differed on shrinking versus stable lakes (Fig. 3). Model selection results for Amphipoda and Corixidae were unequivocal, providing zero support for models lacking the decade*extent interaction (w_i = 0; Table 3); only models with this interaction term allowed for differential decadal variation across shrinking versus stable lakes. Moreover, decade*extent parameter estimates for Amphipoda and Corixidae were large, negative, and well-estimated, indicating substantial losses in abundance on both shrinking and stable lakes over time (Table 4). Specifically, abundance of Amphipoda declined by 95% on shrinking lakes versus 74% on stable lakes, while Corixidae declined by 42% on shrinking versus 73% on stable lakes. Overall, decadal losses in abundance for Amphipoda were the most pronounced of the 6 invertebrate groups examined.

Waterbirds

Probability of lake occupancy for 10 species of adult waterbirds did not differ from 1985–1989 to 2010–2012 (Fig. 4). For all 10 species, 95% BCI from 1985–1989 broadly overlapped those from 2010–2012. Moreover, overlapping credible intervals were not driven by poor precision, as

9 of 10 species had 95% BCI with a range of ≤0.28 for each decade. Likewise, with the exception of Ring-necked Ducks, point estimates of occupancy probability were remarkably steady across decades, differing by <0.10 from 1985–1989 to 2010–2012. For adult Ring-necked Ducks, the point estimate of occupancy probability in 1985–1989 (ψ = 0.21) was markedly lower than that observed in 2010–2012 (ψ = 0.47). However, 95% BCI for the 1980s were imprecise (95% BCI = 0.02, 0.71) and widely overlapped those of the 2010s (95% BCI = 0.47, 0.56), primarily due to poor detection probability (p = 0.10) during the 1980s (Table 5).

Similar to adult waterbirds, probability of lake occupancy for 10 species of waterbird chicks did not significantly differ from 1985–1989 to 2010–2012 (Fig. 5). The 95% BCI from 1985–1989 overlapped those from 2010–2012 for all 10 species. However, 95% BCI were generally less precise than for adults, especially for Mallard, Northern Shoveler, and Ring-necked Duck. Likewise, for all 10 waterbird species, probabilities of detection for chicks (Table 6) were considerably lower than those of adults.

4.5 Discussion

Using an exceptional historic database that benchmarked past lake conditions, we found that lakes with significant losses in surface area did not exhibit unique changes, relative to stable lakes, in chlorophyll concentrations, aquatic invertebrate abundance, or waterbird distributions. These results, which spanned 3 successive trophic levels, suggest that long-term chemical changes on shrinking lakes of the Subarctic did not trophically propagate through lake ecosystems. Moreover, our results occurred despite the pronounced magnitude of chemical changes, including increased concentrations of >200% for total nitrogen, >100% for total phosphorus, >40% for calcium, >500% for chloride, >50% for magnesium, and >100% for

sodium (Lewis et al. 2015a). While our findings depict 2 snapshots of lake environments in the 1980s and 2010s, each decadal sampling period consisted of at least 3 years of data from 55 lakes, suggesting a prevailing ecological pattern that overrides lake-to-lake and year-to-year variation. Furthermore, our BACI study design provides a high level of inference strength, being based on shrinking and stable lakes that were measured both before and after reductions in lake surface area.

Under our bottom-up trophic framework, the minimal influence of rising chemical concentrations on trophic dynamics starts at the base of the food web with primary producers. At this trophic level, we observed that phytoplankton stocks, as indexed by chlorophyll concentrations, remained largely unchanged on both shrinking and stable lakes from 1985–1989 to 2010–2012. This result was unexpected given the large magnitude of nutrient enrichment on shrinking lakes, along with previous studies that observed increased algal production following artificial fertilization of high-latitude lakes and streams (Peterson et al. 1993, Slavik et al. 2004, O'Brien et al. 2005). Artificial fertilization studies, however, typically use chemical forms of nutrients that are readily bioavailable and quickly incorporated into aquatic food webs, such as inorganic nitrates and phosphates. In contrast, nutrients on our study lakes were measured as total nitrogen and total phosphorus, which includes all chemical forms irrespective of their bioavailability. If most of the nutrient gains on shrinking lakes were composed of recalcitrant chemical forms that were unavailable to phytoplankton, then this may primarily explain our observed lack of change in chlorophyll levels. Conversely, nutrient gains may have been largely bioavailable, with requisite increases in phytoplankton production, yet our temporal sampling design failed to capture such increased production. Our chlorophyll measurements, being monitored on a semi-weekly basis, provided periodic snapshots of standing phytoplankton

stocks. However, in shallow, eutrophic lakes such as ours, grazing zooplankton can filter the entire water column 1–2 times per day, depressing standing stocks of phytoplankton even though their rates of production may be high (Lampert et al. 1986, Hanson and Butler 1994). Thus, phytoplankton production on shrinking lakes may have hypothetically increased in response to nutrient enrichment, but remained unapparent in our samples due to rapid phytoplankton turnover by zooplankton grazers. Previous research from our study area suggested that standing phytoplankton stocks were depressed relative to actual production, mainly due to heavy grazing by large-bodied zooplankton that thrived in the absence of fish (Heglund and Jones 2003, Corcoran et al. 2009). Finally, nutrient enrichment on shrinking lakes, while having minimal impact on phytoplankton, may have positively impacted primary producers that our study did not monitor, such as macrophytes and epiphyton. For example, research from Arctic lakes in Alaska found that the aquatic plants *Carex aquatilis* and *Arctophila fulva*, both of which are common in the Yukon Flats, dominated in-lake primary production, especially relative to phytoplankton (Lougheed et al. 2011).

Further up the trophic chain, we found large changes in invertebrate abundance from 1985–1989 to 2010–2012, including decreased abundance of 5 of the 6 groups we examined: Amphipoda, Coleoptera, Corixidae, Gastropoda, and Odonata. These decadal changes, however, were not limited to shrinking lakes, occurring on lakes with stable surface areas as well. This pattern suggests that lakes of the Yukon Flats, irrespective of changes in their surface area or water chemistry, have undergone a systematic loss of invertebrate abundance. Moreover, such pervasive losses in abundance suggest a likewise pervasive cause, especially given the large spatial scale (~900,000 ha) from which our study lakes were located (Fig. 1). Foremost, summer temperatures at northern latitudes have increased by at least twice the global average warming

(New et al. 2011), including significantly higher summer air temperatures in the Yukon Flats over the last 2 to 3 decades (Anderson et al. 2013, Jepsen et al. 2013a). Warmer air temperatures have likely driven concurrent increases in lake water temperatures, including higher summer maxima (Lougheed et al. 2011). Such aquatic warming may be especially pronounced in our shallow study lakes because of their high surface to volume ratios, closed basins, and nearly 24 hour solar incidence during summer. Additionally, although straddling the Arctic Circle, summer air temperatures in the Yukon Flats are warmer than any other comparable latitude in North America, occasionally exceeding 37 °C. For aquatic invertebrates, recently increased water temperatures may more commonly exceed their physiological tolerances than during previously cooler decades, potentially causing losses in abundance over time (Wrona et al. 2006). In particular, warm water holds less dissolved oxygen, causing oxygen stress that can be directly lethal for aquatic invertebrates, or increase their susceptibility to other environmental stresses (Sprague 1963, Pörtner 2002, Wrona et al. 2006). In addition to their high temperatures, our study lakes may be further prone to deoxygenation because of their stagnant water, high loads of rotting aquatic vegetation, and semi-brackish salinity.

While 5 of 6 invertebrate groups declined in abundance over time, Chironomidae larvae increased in abundance by approximately 190% from 1985–1989 to 2010–2012. Chironomidae are among the most tolerant of aquatic invertebrates to temperature and oxygen extremes, commonly serving as bioindicators of water quality (Saether 1979, Ferrington 2008, Lencioni et al. 2012). Much of this tolerance stems from their remarkable diversity, which often exceeds 80 or more species per site in the Nearctic (Ferrington 2008). As lakes undergo state transitions, for example shifting towards high temperature or low oxygen conditions, the high diversity of Chironomidae increases the likelihood that a species will be present that can thrive in the new

conditions. On lakes of the Yukon Flats, significantly higher summer air temperatures, as discussed above, have likely increased water temperatures, with potential for episodic hypoxia. These changes to lake environments, while negatively impacting most invertebrate groups, may have favored certain species of Chironomidae tolerant to such conditions, leading to our observed increase in Chironomidae abundance.

As opposed to purely biological reasons, our observed changes in invertebrate abundance may, in part, result from unknown differences in our sampling protocol across decades. We attempted to exactly replicate methodologies for invertebrate collections from 1985–1989 to 2010–2012, which involved pulling a sweep net horizontally for 1 m just below the water surface and through aquatic vegetation. However, potential decadal differences in sampling procedures, such as removal of invertebrates from the net, sweep length, and sweep depth, may have unknowingly occurred. Such hypothetical sampling differences, if consistent across decades, would ultimately manifest via our estimates of invertebrate abundance, including increased distance between 1980s versus 2010s estimates. As well, some covariates from our 1980s invertebrate database were lost over time, including intra-annual sample date and vegetation type. Again, if these covariates unknowingly differed across decades, then their omission from our analyses may have influenced our decadal estimates of invertebrate abundance. Overall, however, the sheer magnitude of changes, including losses in abundance of >70% for Gastropoda, Coleoptera, and Amphipoda, suggests a real temporal shift in invertebrate abundance that cannot be solely attributed to differences in sampling methods.

At the top of the food web, we observed that distributions of waterbirds, including adults and chicks, remained largely unchanged from 1985–1989 to 2010–2012. While our waterbird data did not allow us to analytically separate stable versus shrinking lakes, the remarkable

stability of our occupancy estimates across decades suggests that losses in surface area had, at most, minimal impact on waterbird distributions. Moreover, this decadal stability in occupancy probability was notably consistent, spanning 10 species of waterbirds. Viewed from an ecosystem perspective, our waterbird results fit our overall observation that chemical changes on shrinking lakes did not initiate a series of trophic cascades. That is, shrinking and stable lakes displayed similar ecosystem trends, extending from phytoplankton to invertebrates to waterbirds. Nonetheless, the decadal stability in waterbird occupancy was somewhat unexpected in view of the wide-ranging losses in invertebrate abundance in our study lakes. In the absence of fish, waterbirds are the top predators on our study lakes during summer, feeding primarily on aquatic invertebrates (Lewis et al. 2015b). Thus, losses in invertebrate abundance, while of a significant magnitude, appear to have had minimal impact on waterbirds to date. Waterbird occupancy rates, however, while sensitive to prey abundance on our study lakes (Lewis et al. 2015b), may not fully capture the potential impact of invertebrate declines on waterbird populations (Johnson 2007). Instead, variables measured at the level of individual birds, such as survival, body condition, and reproductive success, may have been negatively impacted by our observed declines in invertebrate abundance and would thus merit future monitoring (Johnson 2007).

Of the losses in invertebrate abundance, the major declines in amphipod numbers, exceeding 70% on stable lakes and 90% on shrinking lakes, are the most concerning for waterbirds. Recent research suggested that long-term declines in body condition of migrating Lesser Scaup along the Mississippi flyway resulted from landscape-scale reductions in amphipod numbers (Anteau and Afton 2004). Our amphipod data also continue a trend observed 10 years earlier on 9 of our study lakes, in which amphipod biomass decreased by approximately 40–80% (Corcoran et al. 2009). Amphipods are important constituents of secondary production in aquatic

food webs, especially in lakes of the Yukon Flats where their densities average 220/m^3 and occasionally surpass 1000/m^3 (Lewis et al. 2015b). These exceptional densities, along with their high biomass per unit length and favorable energy density, make amphipods important prey of waterbirds and other top predators (Gardner et al. 1985, Fredrickson and Reid 1998). On our study lakes, occupancy rates of 3 abundant waterbird species (Lesser Scaup, Horned Grebes, and White-winged Scoters) were strongly and positively related to amphipod density, while being unrelated to all other invertebrate taxa. Moreover, species richness of waterbirds on our study lakes increased 5-fold across the range of observed amphipod densities, from 2–3 to >15 species (Lewis et al. 2015b). While we did not observe long-term changes in lake occupancy rates of waterbirds to date, continued losses in amphipod abundance may pose a significant threat to waterbirds of the Yukon Flats in the near future.

Finally, we presented decadal estimates of lake occupancy rates for waterbirds, as opposed to estimates of abundance, to examine impacts of long-term habitat changes. For large study populations, occupancy rates can, at times, be unresponsive to changing habitat conditions, mainly because large numerical changes in abundance may have little impact on presence/absence (MacKenzie et al. 2006). Our study lakes, however, were generally small, with a mean surface area of 13 ha, and supported likewise small waterbird populations; e.g., for 8 of 10 species, counts averaged <7 adults and <1 chick per lake. Such small lakes and low counts allow lake occupancy rates to rapidly change in accordance with shifting lake habitats, as opposed to large lakes that harbor likewise large waterbird populations. Moreover, for our surveys where it was difficult or impossible to view all birds at a lake simultaneously, occupancy estimates are less prone to bias from double-counting than are estimates of abundance (Gregory

et al. 2004). Double-counting was especially problematic on lakes which required canoe surveys because our presence on the water continually redistributed waterbirds across the lake.

Overall, we observed that ecosystems of Yukon Flats lakes were largely resilient to rising chemical concentrations associated with long-term losses in surface area. While decadal changes to ecosystems were observed, most notably for aquatic invertebrates, these changes were not exclusive to shrinking lakes, following similar paths on lakes with stable surface areas and little long-term chemical change. This apparent resilience, however, cannot be reliably extrapolated into the future, primarily owing to sustained climatic warming that may further impact surface area and water chemistry of northern lakes. Often, lake ecosystems exhibit an impressive degree of resilience up to some threshold, after which they undergo abrupt changes to alternative states (Carpenter 2003). For our study lakes, and lakes of similar Arctic and Subarctic regions, this hypothetic threshold may be quickly approaching given the high magnitude of chemical changes that have already occurred.

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4.8 Figures

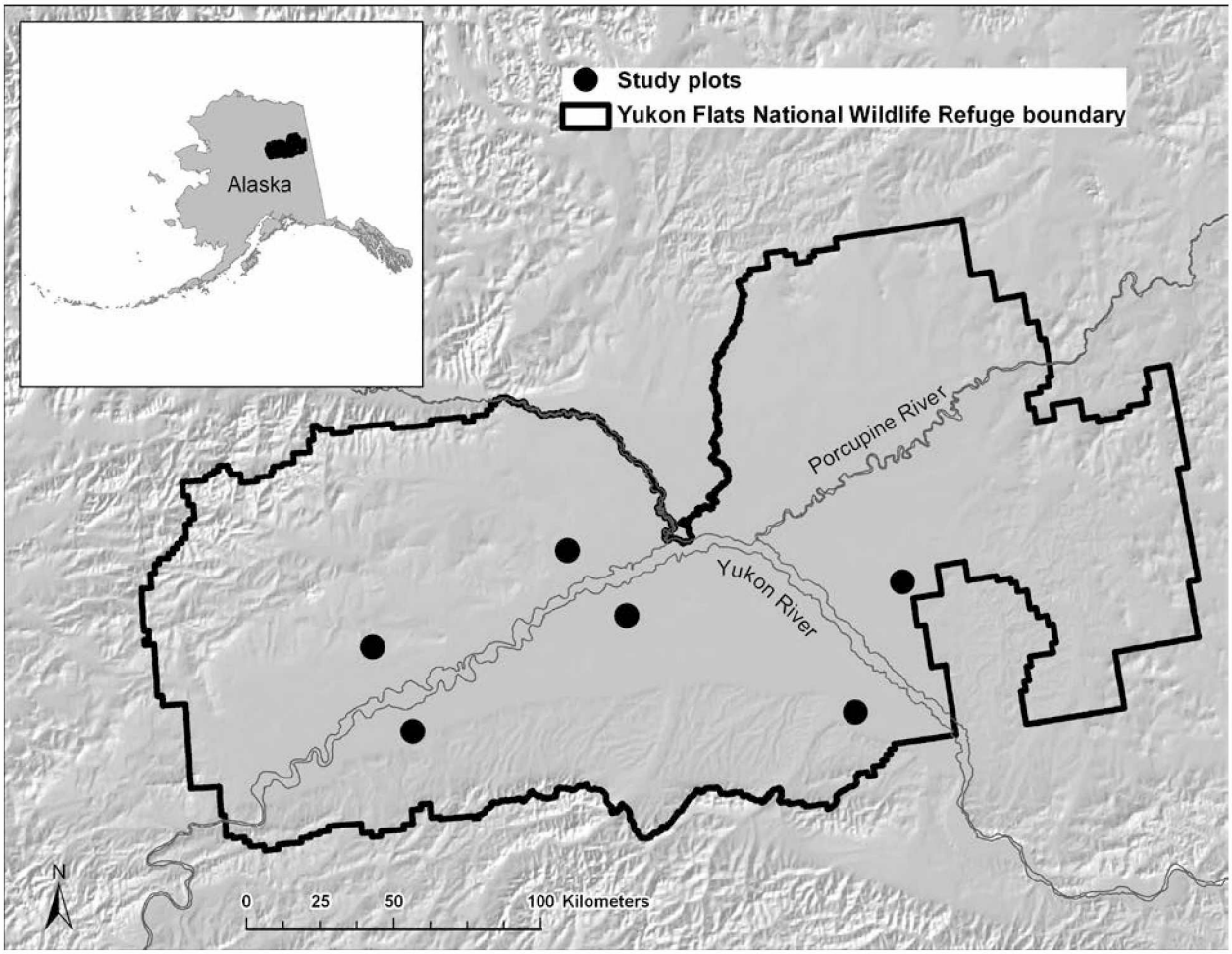

Figure 4-1. Map of the study area in the Yukon Flats National Wildlife Refuge, Alaska, showing the location of the 6 study plots.

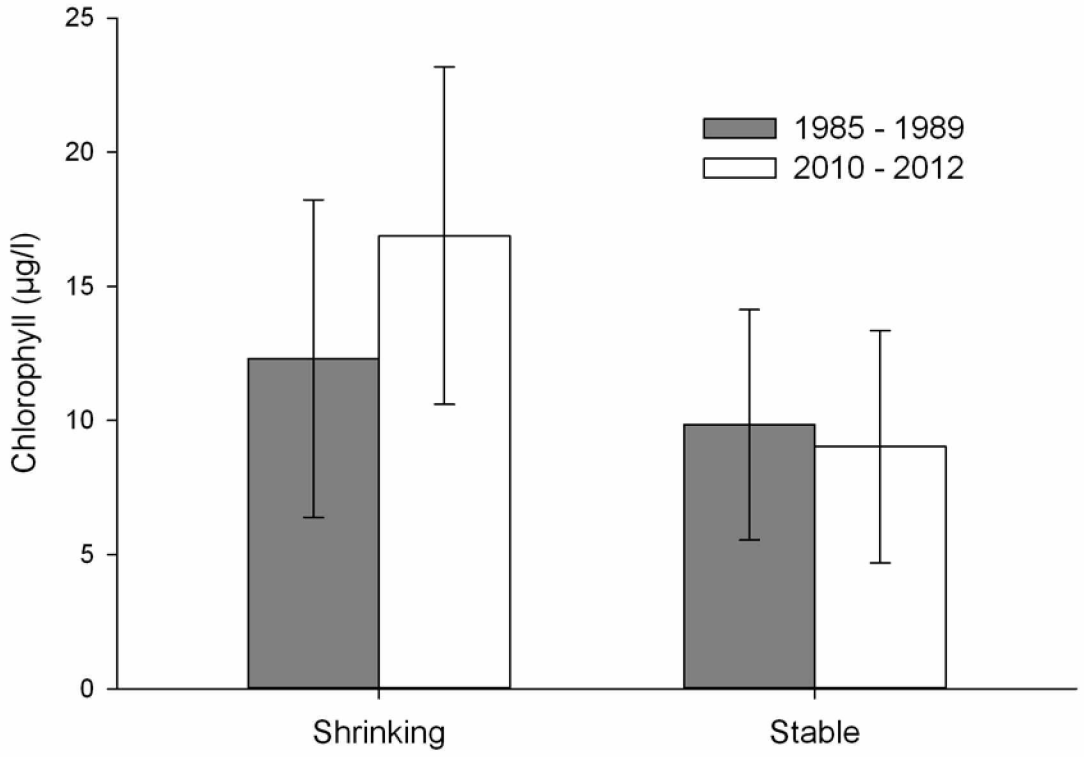

Figure 4-2. Aquatic concentration of chlorophyll (µg/l) for shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data are restricted to lakes with surface areas >1 ha (n =55). Concentrations ± 95% confidence intervals are based on parameter estimates from the global model.

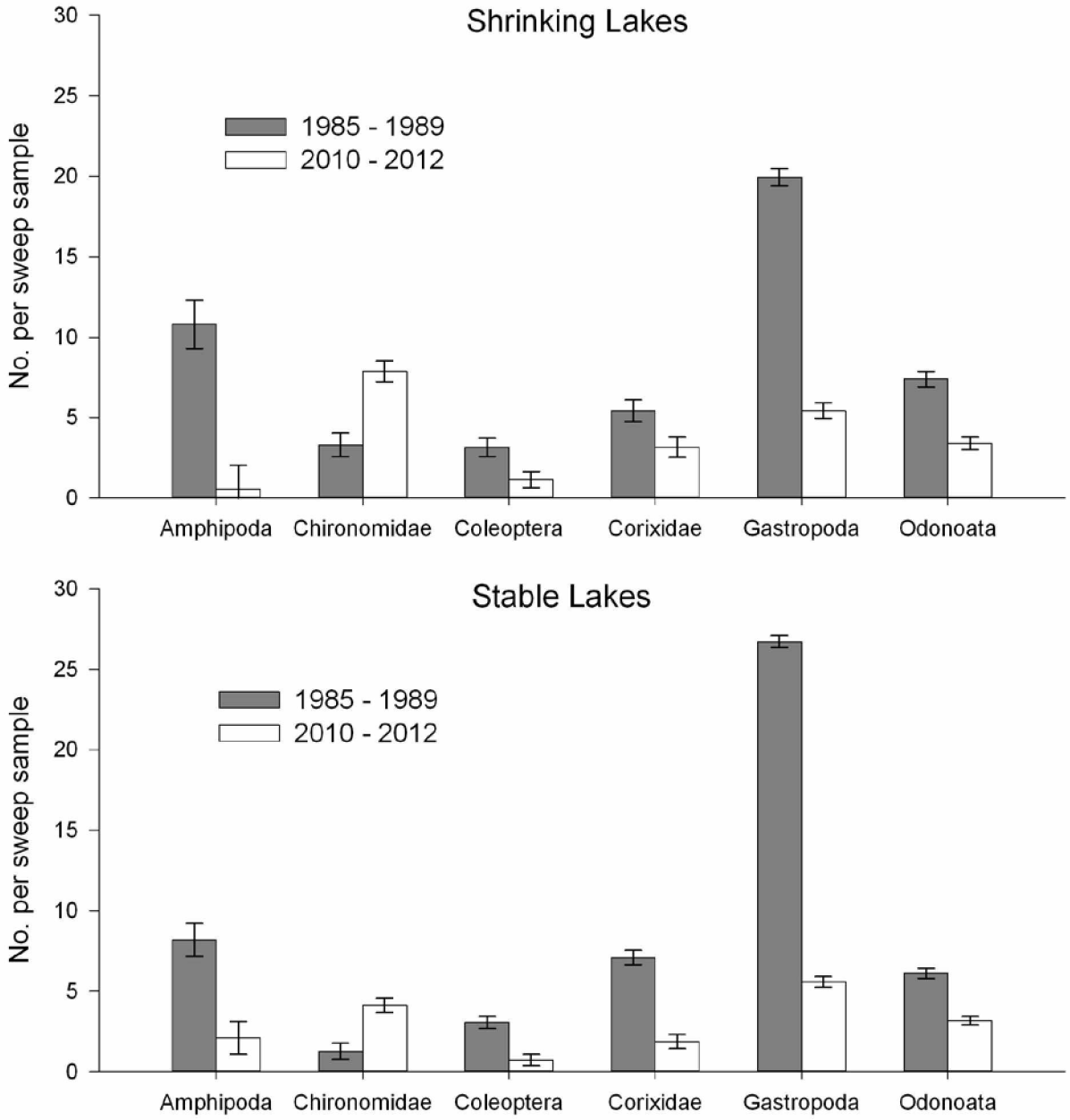

Figure 4-3. Abundance (no./sweep sample) of 6 groups of aquatic invertebrates on shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 vs. 2010–2012. Data are restricted to lakes with surface areas >1 ha (n = 55). Abundance ± 95% confidence intervals are based on parameter estimates from the global model.

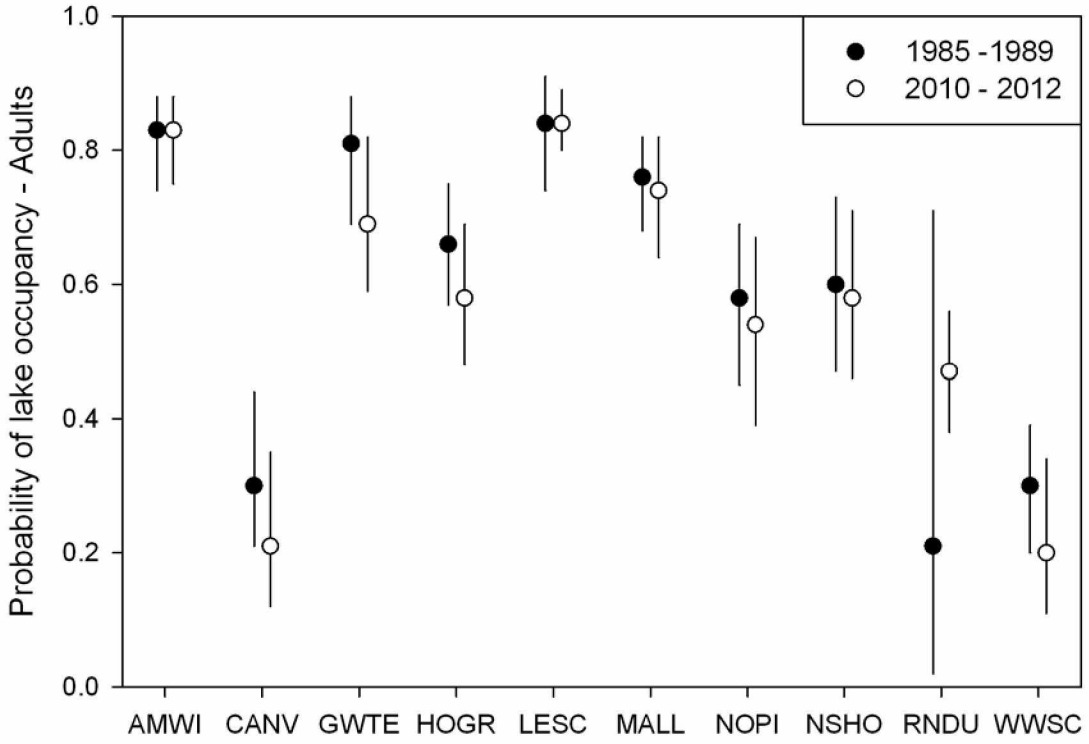

Figure 4-4. Probability of lake occupancy (ψ) ± 95% Bayesian credible intervals for adults of 10 species of waterbirds in the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data includes all study lakes, irrespective of surface area, for a total of $n = 77$ lakes. Waterbird species include American Wigeon (AMWI), Canvasback (CANV), Green-winged Teal (GWTE), Horned Grebe (HOGR), Lesser Scaup (LESC), Mallard (MALL), Northern Pintail (NOPI), Northern Shoveler (NSHO), Ring-necked Duck (RNDU), and White-winged Scoter (WWSC).

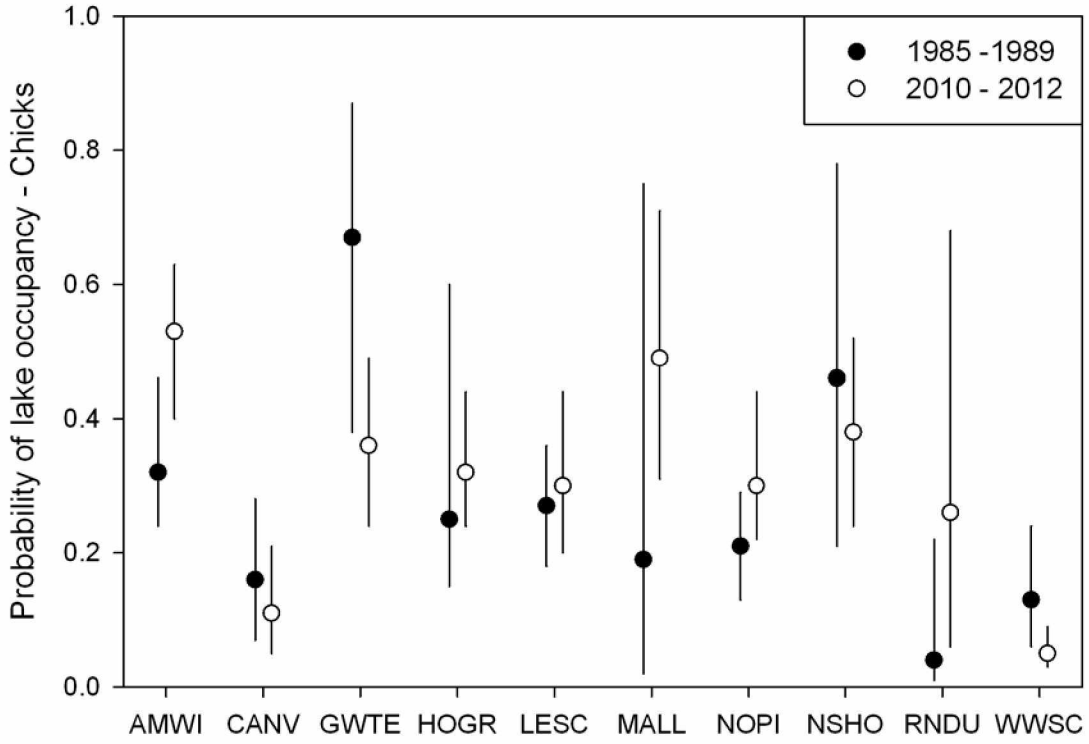

Figure 4-5. Probability of lake occupancy (ψ) ± 95% Bayesian credible intervals for chicks of 10 species of waterbirds in the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data includes all study lakes, irrespective of surface area, for a total of $n = 77$ lakes. Waterbird species include American Wigeon (AMWI), Canvasback (CANV), Green-winged Teal (GWTE), Horned Grebe (HOGR), Lesser Scaup (LESC), Mallard (MALL), Northern Pintail (NOPI), Northern Shoveler (NSHO), Ring-necked Duck (RNDU), and White-winged Scoter (WWSC).

4.9 Tables

Table 4-1. Model selection results from linear mixed models describing variation in chlorophyll concentration (µg/l) on shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Models are listed in order of ΔAIC and we also present number of parameters (k) and model weights (w_i). Data are restricted to lakes with surface areas >1 ha (n =55). Covariates include Ordinal (intra-annual date), Decade (1980s vs. 2010s), Extent (shrinking vs. stable), and a Decade*Extent interaction.

Model	ΔAIC	k	w_i
Ordinal + Extent	0	5	0.59
Ordinal + Decade + Extent	1.80	6	0.24
Ordinal + Decade + Extent + Decade*Extent	2.45	7	0.17
Ordinal + Decade	3415.27	5	0
Null	3415.59	3	0

Table 4-2. Model-averaged parameter estimates (Est), unconditional standard errors, and lower (LCI) and upper (UCI) 95% confidence intervals from linear mixed models describing variation in chlorophyll concentration (µg/l) on shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data are restricted to lakes with surface areas >1 ha (*n* =55). Covariates include Ordinal (intra-annual date), Decade (1980s vs. 2010s), Extent (shrinking vs. stable), and a Decade*Extent interaction.

Covariate	Est	SE	LCI	UCI
Intercept	4.41	7.56	-10.41	19.23
Ordinal	0.05	0.04	-0.02	0.12
Decade [a]	2.50	3.47	-4.30	9.30
Extent [a]	-4.54	3.28	-10.98	1.89
Decade*Extent [a]	-5.41	4.65	-14.52	3.70

[a] Reference values: Decade – 2010s; Extent – Stable; Decade*Extent – 2010s*Stable

Table 4-3. Model selection results from generalized linear mixed models describing variation in abundance (no./sweep sample) of 6 groups of aquatic invertebrates on shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Models are listed in order of ΔAIC and we also present number of parameters (k) and model weights (w_i). Data are restricted to lakes with surface areas >1 ha (n =55). Covariates include Decade (1980s vs. 2010s), Extent (shrinking vs. stable), and a Decade*Extent interaction.

Invertebrate	Model	ΔAIC	k	w_i
Amphipoda	Decade + Extent + Decade*Extent	0	6	1.00
	Decade	43.82	4	0
	Decade + Extent	44.66	5	0
	Null	397.86	3	0
	Extent	399.50	4	0
Chironomidae	Decade + Extent + Decade*Extent	0	6	0.50
	Decade + Extent	0.32	5	0.42
	Decade	3.67	4	0.08
	Extent	117.39	4	0
	Null	120.51	3	0
Coleoptera	Decade + Extent + Decade*Extent	0	6	0.73
	Decade + Extent	3.31	5	0.14
	Decade	3.47	4	0.13
	Extent	332.48	4	0
	Null	333.00	3	0
Corixidae	Decade + Extent + Decade*Extent	0	6	1.00
	Decade	18.79	4	0
	Decade + Extent	19.59	5	0
	Null	307.78	3	0
	Extent	309.13	4	0
Gastropoda	Decade	0	4	0.55
	Decade + Extent + Decade*Extent	1.62	6	0.24
	Decade + Extent	1.90	5	0.21
	Null	501.93	3	0
	Extent	503.81	4	0

Table 4–3 (continued)

Invertebrate	Model	ΔAIC	k	w_i
Odonata	Decade	0	4	0.63
	Decade + Extent	1.79	5	0.26
	Decade + Extent + Decade*Extent	3.31	6	0.12
	Null	83.14	3	0
	Extent	84.88	4	0

Table 4-4. Model-averaged parameter estimates (Est) and standard errors (SE) from generalized linear mixed model describing variation in abundance (no./sweep) of 6 groups of aquatic invertebrates on shrinking and stable lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. We indicated estimates with 95% confidence intervals that did not include 0 with an asterisk (*). Data presented in this table are restricted to lakes with surface areas > 1 ha (n = 55). Covariates include Decade (1980s, 2010s), Extent (shrinking, stable, expanding), and a Decade*Extent interaction.

	Amphipoda		Chironomidae		Coleoptera		Corixidae		Gastropoda		Odonata	
Covariate	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE	Est	SE
Intercept	2.38*	0.76*	1.06*	0.35*	1.19*	0.27*	1.69*	0.35*	3.15*	0.20*	1.92*	0.17*
Decade[a]	-2.96*	0.20*	0.97*	0.17*	-1.11*	0.17*	-0.54*	0.16*	-1.46*	0.10*	-0.70*	0.11*
Extent[a]	-0.28	0.93	-0.82	0.42	-0.08	0.35	0.27	0.42	0.19	0.31	-0.12	0.26
Decade*Extent[a]	1.60*	0.24*	0.31	0.26	-0.42	0.22	-0.79*	0.19*	-0.26	0.19	0.12	0.21

[a]Reference values for categorical parameters: Decade – 2010s; Extent – stable; Decade*Extent – 2010s*stable.

Table 4-5. Probability of detection (p) and lower (LBCI) and upper (UBCI) 95% Bayesian credible intervals for 10 species of adult waterbirds on lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data includes all study lakes, irrespective of surface area, for a total of $n = 77$ lakes.

	1985–1989			2010–2012		
Waterbird species	p	LBCI	UBCI	p	LBCI	UBCI
American Wigeon	0.64	0.60	0.68	0.64	0.58	0.69
Canvasback	0.42	0.35	0.47	0.49	0.39	0.58
Green-winged Teal	0.54	0.48	0.58	0.59	0.54	0.65
Horned Grebe	0.57	0.53	0.62	0.70	0.65	0.75
Lesser Scaup	0.65	0.61	0.69	0.66	0.62	0.71
Mallard	0.51	0.46	0.57	0.63	0.57	0.68
Northern Pintail	0.59	0.55	0.64	0.53	0.47	0.60
Northern Shoveler	0.57	0.52	0.62	0.60	0.54	0.65
Ring-necked Duck	0.10	0.02	0.22	0.58	0.52	0.65
White-winged Scoter	0.54	0.48	0.60	0.51	0.44	0.61

Table 4-6. Probability of detection (p) and lower (LBCI) and upper (UBCI) 95% Bayesian credible intervals for 10 species of waterbird chicks on lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012. Data includes all study lakes, irrespective of surface area, for a total of $n = 77$ lakes.

	1985–1989			2010–2012		
Waterbird species	p	LBCI	UBCI	p	LBCI	UBCI
American Wigeon	0.31	0.25	0.39	0.45	0.37	0.55
Canvasback	0.26	0.18	0.35	0.45	0.36	0.59
Green-winged Teal	0.12	0.08	0.18	0.35	0.23	0.45
Horned Grebe	0.21	0.09	0.33	0.65	0.51	0.93
Lesser Scaup	0.29	0.23	0.37	0.69	0.57	0.79
Mallard	0.06	0	0.19	0.35	0.25	0.42
Northern Pintail	0.18	0.13	0.23	0.37	0.28	0.44
Northern Shoveler	0.10	0.05	0.16	0.24	0.18	0.32
Ring-necked Duck	0.44	0	0.95	0.58	0.13	1
White-winged Scoter	0.22	0.14	0.34	0.68	0.48	0.93

Chapter 5

Multi-trophic resilience of boreal lake ecosystems to forest fires[1]

5.1 Abstract

Fires are the major natural disturbance in the boreal forest, and their frequency and intensity will likely increase as the climate warms. Terrestrial nutrients released by fires may be transported to boreal lakes, stimulating increased primary productivity, which may radiate through multiple trophic levels. Using a before-after-control-impact (BACI) design, with pre- and post-fire data from burned and unburned areas, we examined effects of a natural fire across several trophic levels of boreal lakes, from nutrient and chlorophyll levels to macroinvertebrates to waterbirds. Concentrations of total nitrogen and phosphorus were not affected by the fire. Chlorophyll *a* levels were also unaffected, likely reflecting the stable nutrient concentrations. For aquatic invertebrates, we found that densities of 3 functional feeding groups did not respond to the fire (filterers, gatherers, scrapers), while 2 groups increased (shredders, predators). Amphipods accounted for 98% of shredder numbers, and we hypothesize that fire-mediated habitat changes may have favored their generalist feeding and habitat ecology. This increase in amphipods may have in turn driven increased predator densities, as amphipods were the most numerous invertebrate in our lakes and are commonly taken as prey. Finally, abundance of waterbird young, which feed primarily on aquatic invertebrates, was not affected by the fire. Overall, ecosystems of our study lakes were largely resilient to forest fires, likely due to their high initial nutrient concentrations and small catchment sizes. Moreover, this resilience spanned multiple

[1] Lewis, T.L., M.S. Lindberg, J.A. Schmutz, and M.R. Bertram. 2014. Multi-trophic resilience of boreal lake ecosystems to forest fires. Ecology 95:1253–1263

trophic levels, a significant result for ecologically similar boreal regions, especially given the high potential for increased fires with future climate change.

5.2 Introduction

Fires are one of the most widespread and severe disturbances in many ecosystems, and thereby play an important role in regulating ecosystem structure and function. Although a terrestrial disturbance in origin, the effects of fires extend to aquatic ecosystems via cross-habitat transfers of energy and nutrients (Bisson et al. 2003). Fires release nutrients and organic matter locked in terrestrial resources such as soils and vegetation, making them available for transport to aquatic ecosystems. Yields of nitrogen and phosphorus, the two most commonly limiting nutrients for vegetative growth, frequently increase in aquatic systems following fires (Carignan et al. 2000, McEachern et al. 2000). Depending on fire and catchment characteristics, nutrient increases can be quite dramatic; following a forest fire in a pristine catchment, aquatic nitrate increased 9-fold, total nitrogen 2-fold, and total phosphorus 4-fold (Kelly et al. 2006). Importantly, this flux of energy and nutrients from terrestrial to aquatic habitats, known as an ecological subsidy (Polis et al. 2004), may be a significant driver of aquatic productivity across several trophic levels

At the outset, elevated aquatic nutrients often stimulate primary productivity, typically evident via increased phytoplanktonic and benthic chlorophyll *a* (Scrimgeour et al. 2001, Kelly et al. 2006). Increased primary production may in turn drive increases in secondary production of aquatic herbivores, which are often dominated by invertebrates in freshwater systems (Malison and Baxter 2010a). Aquatic invertebrates in Canadian lakes had greater biomass in burned versus unburned areas, and this persisted 15–20 years post-fire (Scrimgeour et al. 2001). However, changes in secondary consumer communities following fires are difficult to generalize and are

typically related to the stochastic nature of fire disturbance, as well as the ecology of the impacted invertebrates (Minshall 2003). For example, shredders in streams may decline post-fire due to the loss of allochthonous leaf detritus, while scrapers may thrive in response to increased periphyton growth (Minshall 2003, Mellon et al. 2008). Finally, consumers specializing on aquatic invertebrates may also benefit from forest fires, as the pulse of aquatic productivity travels up trophic levels. Fish growth rates were 12–30% greater following a forest fire, presumably in response to increased abundance of invertebrate food sources (Kelly et al. 2006). In the boreal forest, fires are the major natural disturbance and their long-term frequency and intensity are predicted to increase as the climate warms (Chapin et al. 2008). The area burned in the North American boreal forest tripled from the 1960s to 1990s, mainly because of an increased frequency of extreme fire years (Kasischke and Turetsky 2006). During the 1990s and 2000s alone, >25% of Alaska's boreal forest burned (Kasischke et al. 2010). Because much of the boreal forest lies in the permafrost zone, effects of boreal fires on aquatic ecosystems may be especially pronounced. Permafrost stores large amounts of organic carbon and nutrients that are largely removed from active biogeochemical cycling; however, by removing the vegetative layers that insulate the ground, fires may accelerate thawing of permafrost and subsequent activation of its stored organic matter (O'Donnell et al. 2011). Thus, in addition to aboveground biomass released during the fire, boreal fires may also increase the release and transport of permafrost-associated nutrients, some of which may ultimately enrich aquatic ecosystems.

Boreal wetlands and lakes account for approximately 50% of global lake surface area (Schindler 1998) and are internationally important bird areas, annually supporting >15 million breeding waterbirds in North America. Nonetheless, little is known of fire impacts on boreal lakes, especially those impacts on aquatic food webs. Boreal lakes often support complex food

webs that span multiple trophic levels. Many of these lakes are shallow and, because of the harsh winter climate, freeze to or near the benthos, effectively excluding fish populations (Bayley et al. 2007). Fishless lakes support more abundant and complex populations of aquatic invertebrates due to the relaxation of piscine predation (Bendell and McNicol 1987). These lakes are especially important for breeding waterbirds because aquatic invertebrates are the primary food source for rapidly growing waterbird chicks (DesGranges and Gagnon 1994).

In this study, we ask: does a natural forest fire release sufficient nutrients to stimulate eutrophication of boreal lakes, and if so, does this enrichment transfer across trophic levels such that each level experiences increased productivity? To answer this question, we studied the effects of a natural wildfire on lakes of the Yukon Flats, a pristine boreal forest basin in Alaska that annually supports >1 million breeding waterbirds. The Yukon Flats is one of the most flammable boreal regions in North America and charcoal records indicate the area has shifted into a new regime of unprecedented fire activity, with fire frequency from the most recent decades far surpassing that of the past 10,000 years (Kelly et al. 2013). Of our 14 study lakes on the Yukon Flats, 7 were largely surrounded by burned forest while 7 were not, fortuitously creating a robust study design in which lakes in unburned areas served as in-site controls. Further, all lakes were sampled the summer preceding the fire, allowing us to use a before-after-control-impact (BACI) study design where pre-fire data serves as the baseline at each lake (Morrison et al. 2008). By employing pre-fire data, the BACI design avoids the inference threat common to most wildfire studies, in which differences between burned and unburned sites may be unrelated to the fire, having existed beforehand. Under this design, which is rarely available for naturally occurring fire events such as ours, we provide the first known data describing multi-trophic effects of a forest fire on boreal lake ecosystems. Specifically, we tested four successive

predictions: (1) total nitrogen and phosphorus will increase more in burned versus unburned areas following the fire, (2) chlorophyll concentrations in burn-affected lakes will be stimulated by increased nutrient levels, (3) aquatic invertebrate abundance in burn-affected lakes will positively respond to heightened nutrient and chlorophyll levels, and (4) abundance of waterbird chicks will respond to increased invertebrate abundance, being greater on lakes in burned areas.

5.3 Materials and Methods

Study site

The Yukon Flats is a large basin (~30,000 km^2) in interior Alaska that contains >40,000 lakes and wetlands and is largely pristine natural habitat. The area is underlain by discontinuous permafrost, has low landscape relief, and supports a mixed boreal forest dominated by black (*Picea mariana*) and white spruce (*P. glauca*), Alaska birch (*Betula neoalaskana*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and willow (*Salix* spp.). Our study site (66.4°N, 148.3°W) contained 14 study lakes spread across 16 km^2. Lakes varied in size from 5000 to 600,000 m^2, but were uniformly shallow, never measuring deeper than 2 m. All study lakes functioned largely as closed-basins, with no well-defined surface inlets or outlets. This combination of shallow depth and lack of outlets precluded fish populations in all lakes. In Sept 2010, a lightning ignited fire burned a large portion of the study site. Satellite data from Monitoring Trends in Burn Severity (www. mtbs.gov) was available for approximately half our study area and classified the burn severity as 55% moderate, 19% high, 18% low, and 8% unburned. The fire removed most standing vegetation in the burned areas and, in some instances, the peat and upper organic soil layers were also consumed, leaving behind bare mineral soils. See appendix A for map and images of burned and unburned boreal habitats in the study area.

Lake Classification

We classified each lake as either burned or unburned and hereafter use this terminology throughout. We were unable to categorize lakes based on extent of spatial overlap between their catchments and the fire; lake catchments were unknown because of the extremely low relief of the study area (<10 m) and the lack of defined inlets draining into lakes. In its place, we digitally added a 200 m buffer around the perimeter of each lake and then estimated spatial overlap between buffers and the fire to classify lakes as burned (>55% of buffer was burned; 7 lakes) or unburned (<25% of buffer was burned; 7 lakes). Geospatial borders for lakes and fires were acquired from the National Hydrography Dataset and Alaska Interagency Coordination Center, respectively. The 200 m buffer was used because it was the maximum size at which buffers did not grossly extend into the surface area, and thereby catchments, of neighboring lakes. Also, because buffers conformed to lake perimeters, the total area encompassed by each buffer was approximately scaled to lake size. Mean percentage (± SD) of buffers within burned forest were 89% ± 19 and 13% ± 12 for burned and unburned lakes, respectively.

Water Chemistry

We sampled water chemistry of each lake once per month (Jun–Aug) per year (2010–12), with the exception of August 2012. We collected 8 liters of water from near the lake's center point and 25 cm below the surface as per prior water sampling protocol developed for the Yukon Flats (Heglund 1992). Our study lakes, because of their shallow depth, are frequently mixed and thermal stratification is ephemeral (Heglund and Jones 2003); thus, the lake's center point provided a relevant location from which to gauge its general water chemistry status, including inputs from terrestrial sources. Water samples were used to measure total nitrogen (TN), total

phosphorus (TP), and chlorophyll *a* (CHL). Three 5 ml aliquots of lake water were acidified on-site with sulfuric acid and stored at cold temperatures for determination of TN. Three un-acidified 5 ml aliquots of lake water, also kept at cool temperatures, were used for TP. For CHL, we filtered measured volumes of lake water on-site through Gelman A/E glass fiber filters until a noticeable algal stain developed on the filter. We collected 2 filters per sample event and filters were immediately placed in protective sleeves, desiccated with silica gel beads, and kept in dark, cool storage until transported to laboratory freezers.

In the lab, TP concentration was determined by colorimetric measurement of orthophosphate following persulfate oxidation (method 4500-PE; APHA 1995). TN concentration was measured by second-derivative spectroscopic analysis of persulfate-oxidized samples (Crumpton et al. 1992). CHL was extracted with 90% ethanol and concentrations were determined with fluorometric methods (Knowlton 1984). Final TN and TP values are averages of the 3 aliquots collected per sample event. Final CHL values are averaged from the 2 filters collected and are corrected for the volume of water passed through each filter. All laboratory analyses were conducted by the Jones Limnology Lab, University of Missouri, Columbia, MO.

Aquatic Invertebrates

Aquatic invertebrates were collected from each lake once per month (Jun–Jul) per year (2010–12). Sampling transects were established at random locations along the perimeter of each lake and oriented perpendicular to shore. Number of transects were scaled to lake area and each lake had a minimum of 2 and a maximum of 13 transects. Abundance and type of aquatic invertebrates are related to aquatic vegetation (Gregg and Rose 1985). Thus, along each transect, we collected one invertebrate sample per unique vegetative zone, and a typical transect contained

2–3 samples. Vegetative zones included both emergent and submergent vegetation, with the most common plants being cattail (*Typha latifolia*), pondweed (*Potamageton* spp.), sedge (*Carex* spp.), and hornwort (*Ceratophyllum demersum*). In the event that ≤1 vegetative zones were encountered, an extra sample was collected in the open water zone. Samples were collected from the water column with a D-frame sweep net (0.5 mm mesh) by pulling it horizontally for 1 m just below the water surface and through the vegetation. Contents of each sweep sample were placed in ethanol and transported to the laboratory for further processing. Invertebrates were identified to minimum taxonomic levels, typically family, and enumerated. Counts were then converted to volumetric densities (individuals/m^3) based on net-frame dimensions and length of sweep.

Waterbird Surveys

We surveyed each lake for waterbirds (ducks and grebes) 1–2 times per month (Jun–Aug) per year (2010–12), with the exception of August 2012. Surveys were timed to cover the breeding cycle, from nesting (early Jun) through brood rearing (late Jun–Aug). Observers recorded species and age (adult vs. chick) of each waterbird observed on the lake. We employed repeat sampling, in which each survey consisted of 2 independent counts conducted over 1–2 days, allowing us to estimate detection probability (Royle 2004; see *Statistical Analyses*). For small lakes which could be surveyed from one viewing location, repeat counts were conducted back-to-back by unique observers. Larger lakes, however, required the observer to move among multiple survey points by canoe, and these movements potentially affected waterbird detection on subsequent counts. Thus, under the assumption that observer-effects decrease with time since survey, we separated repeat counts on large lakes by 24 hrs to establish independence between counts.

Statistical Analyses

The primary goal of our analyses was to determine effects of forest fires on three aspects of aquatic ecology: 1) water chemistry, 2) aquatic invertebrates, and 3) abundance of waterbird chicks. We first analyzed water chemistry data, using the following three response variables: TN, TP, and CHL. For each response variable, we fit an *a priori* set of general linear mixed models using the 'nlme' package in program R (Pinheiro et al. 2013). Our model set was composed of 6 models, one of which was a null intercept-only model. Three models examined temporal patterns in the data without including fire effects, and included a model with 'Year'(2010, 2011, 2012), a model with 'Date' (intra-annual date), and a model with 'Year*Date' interaction. In BACI study designs, a significant effect of the ecological impact appears via the interaction between site (control vs. impact) and time (pre- vs. post-impact); thus, we tested for an effect of fire on water chemistry by including the interaction between 'Fire' (burned vs. unburned) and 'Period' (pre- vs. post-fire) in our final 2 models. Specifically, one model included the 'Fire*Period' interaction and its main effects, while the other included the interaction term, its main effects, and 'Date'. Finally, all models included the random effects of study lake (n = 14) and sample event (n = 8).

For analyses of aquatic invertebrates, we first classified each family by their functional feeding group (filterer, gatherer, predator, scraper, shredder) to improve the ecological interpretation of results. We used raw invertebrate counts (individuals/sample) as response variables in our model sets, which is typically fit with Poisson distribution models. However, our variance was degrees of magnitude larger than the mean, raising doubts as to the appropriateness of Poisson models. Accordingly, we fit our most parameterized model with negative binomial, Poisson, and zero-inflated negative binomial and Poisson distributions, and then compared model fit with AIC. Results indicated that our count data followed a negative binomial

distribution and were not zero-inflated. For each functional feeding group, we fit a candidate set of negative binomial generalized linear mixed models using the 'glmmADMB' package in program R (Skaug et al. 2012). Candidate model sets were identical to those used for our analysis of water chemistry (described above) and included lake as a random effect.

We used N-mixture models (Royle 2004), a type of hierarchical generalized linear model, to determine effects of fires on waterbird abundance (chicks/lake). Analyses were restricted to chicks because, as opposed to adults, they feed primarily on invertebrates, making them more sensitive to changes in invertebrate densities. Our hierarchical models are composed of 2 components: (1) the detection model (p), which estimates detection probability given imperfect detection, and (2) the abundance model (λ), which describes how variation in ecological processes affects abundance. These models are appropriate for our data because the small size and secretive nature of waterbird chicks leads to low probabilities (<0.5) of detection which, if unaccounted for, yield biased and unreliable estimates of abundance (Walker et al. 2013). For abundance, we used an *a priori* set of candidate models identical to that used for water chemistry and invertebrates, with the exception that 'Lake area' was included in each model and itself constituted a one-variable model, for a total of 7 models. These abundance models were paired with counterpart models describing detection: null abundance and detection models occurred together, while the other 6 abundance models were paired with identical detection models that included the variable of 'Observer'. 'Observer' categorically classifies surveyors as experienced or inexperienced. All N-mixture models were fit using maximum likelihood estimation in R package 'unmarked' (Fiske and Chandler 2011). To determine the appropriate distribution of our abundance data, we first fit our most parameterized model with negative binomial, Poisson, and zero-inflated Poisson distributions. Results indicated that the negative binomial distribution

provided the best fit and hence was used in all models of waterbird abundance.

We used an information-theoretic approach to model selection, in which the relative fit of models within a candidate set were compared with Akaike's information Criterion (AIC) and AIC weights (w_i). Inference of fixed effects was based on model selection and precision of parameter estimates. When large standard errors (SE) indicated imprecise parameter estimates, the variable was deemed uninformative. We used model-averaged parameter estimates and unconditional SEs when candidate model sets displayed selection uncertainty, with multiple models being supported by the data. Otherwise, when a clear top model emerged, we used parameter estimates and SEs from the highest-ranked model.

5.4 Results

Water Chemistry

We collected 112 water samples from 14 lakes during 2010–12 and concentrations (µg/l) of TN, TP, and CHL ranged from 1500–3500, 30–120, and 1–25, respectively. TN, TP, and CHL were all unaffected by the forest fire, as their post-fire values remained largely similar to those from the pre-fire period on both burned and unburned lakes (Fig. 1). For all 3 water chemistry variables, models incorporating fire parameters (fire, period, fire*period) received little support ($w_i \leq 0.09$; Appendix B: Table B1) and had imprecise parameter estimates with large SEs (Appendix C: Table C1). The best-fitting model ($w_i = 0.69$) to explain variation in TN contained only date as an explanatory variable; TN increased over the summer, from June–August, then receded back to lower values by the onset of the following summer (Fig. 1). The model containing date*year received moderate support ($\Delta AIC_c = 2.19$), although imprecise parameter estimates for year indicate this support was driven mainly by date (Appendix C: Table C1).

Similarly, date was the only variable receiving support from the CHL model set, although its model weight (w_i = 0.48) indicated a lower level of support than for TN models. CHL concentrations were negatively related to date and generally decreased over the summer period (Fig. 1). Finally, TP concentrations were not well described by any of the explanatory variables used in our models set. The best-supported model (w_i = 0.49) for describing variation in TP was the null model, which fit an intercept only.

Aquatic Invertebrates

We collected 1035 invertebrate samples from 2010–12, containing a total of 78,394 individuals from 55 families. The most common taxa for each functional feeding group, listed in order of abundance, were as follows: filterers – Conchostraca, Ostracoda, Sphaeriidae; gatherers – Chironomidae, Collembola. Baetidae; scrapers – Physidae, Planorbidae, Lymnaeidae; shredders – Amphipoda, Phryganeidae, Leptoceridae; predators – Coenagrionidae, Hirudinea, Dytiscidae.

The fire had little to no effect on densities of filterers, gatherers, and scrapers. For each of these groups, pre- and post-fire densities generally followed similar trajectories across burned and unburned lakes, indicating that changes in densities were not driven by fires (Fig. 2). For gatherers and scrapers, models with fire parameters received almost no support ($w_i \leq 0.06$). For filterers, the model with fire parameters and date received some support (w_i = 0.20), but parameter estimates for fire and fire*period were imprecise (Appendix C: Table C2). Rather, for all 3 groups, the best-supported model ($w_i \geq 0.78$) contained date, year, and date*year. This model indicates that densities of filterers, gatherers, and scrapers are subject to intra- and inter-annual fluctuations, with year 2011 generally supporting higher densities of all 3 groups (Fig. 2).

The fire had a positive effect on densities of shredders and predators. Shredder densities were similar on burned versus unburned lakes prior to the fire. Following the fire, however, shredder densities increased on burned lakes while remaining steady on unburned lakes (Fig. 2). For predators, densities were generally higher post- versus pre-fire on both burned and unburned lakes. However, increases were almost two times more pronounced on burned lakes, as well as more recurrent from month to month (Fig. 2). For both shredders and predators, the best-supported model ($w_i \geq 0.76$) describing variation in density contained fire parameters (fire, period, fire*period) and date (Appendix B: Table B2). Both shredder and predator densities were positively related to date, indicating that densities increased over the summer from June to July (Fig. 2). Finally, predator densities were moderately influenced by year, with the model containing date*year receiving a small level of support ($\Delta AIC = 2.3$). However, because year is confounded with fire, year effects cannot be interpreted without first considering the effects of fire; in this instance, effects of fire appear to supersede those of year.

Waterbird Abundance

We conducted 140 surveys from 2010–12, counting 4070 waterbird chicks from 13 species. Lesser scaup (*Aythya affinis*) and American wigeon (*Anas americana*) were the most numerous species, accounting for 33% and 18% of total chicks, respectively, followed by mallard (*Anas platyrhynchos*; 9%), canvasback (*Aythya valisineria*; 9%), horned grebe (*Podiceps auritus*; 8%), and white-winged scoter (*Melanitta fusca*; 7%). The top model ($w_i = 0.94$) describing variation in chick abundance contained fire parameters (fire, period, fire*period) and date (Appendix B: Table B3). Support for this model, however, was driven by the main effects of fire and period, and not their interaction. This is because the interaction fire*period had a parameter estimate

near zero with a SE more than 3 times as large as the estimate (-0.21 ± 0.73). Viewed without the interaction, the main effect of fire indicates unburned lakes had more chicks than burned lakes, while that of period indicates higher chick abundances pre- versus post-fire (Appendix C: Table C3). However, when we account for the non-significant interaction between fire and period, we observe that (1) higher chick abundances on unburned lakes existed both pre- and post-fire, and (2) higher pre-fire abundances existed on both burned and unburned lakes (Fig. 3). Accordingly, without a significant interaction term, we conclude that the fire had no discernible impact on chick abundance.

Date appeared in all models with a $w_i > 0$ and indicated that chick abundance increased over the summer, which is expected given that a higher proportion of nests have hatched at later dates. Lake area was positively related to chick abundance, with higher abundances on larger lakes. Year received moderate support, largely due to lower chick abundances during summer 2012. Finally, detection probability differed little between experienced versus inexperienced observers, averaging 0.54 ± 0.02. Parameter estimates are presented in Appendix C: Table C3.

5.5 Discussion

Water Chemistry

Contrary to our predicted increase, we found that a large boreal forest fire had minimal effects on aquatic nutrient concentrations in the 2 years immediately following the fire. Likewise, we detected no fire-mediated increase in chlorophyll *a* concentration. This result was expected in view of our observation that TN and TP were not affected by the fire; P, and less so N, commonly limits primary productivity in lakes, such that detectable changes in chlorophyll require concomitant changes in P or N (Schindler 1977). However, while chlorophyll

concentrations can be contextually explained, the lack of post-fire change in TN and TP concentrations requires further exploration.

In general, lakes of the Yukon Flats are nutrient-rich with high biological productivity; of 129 lakes sampled from 1985–89, Heglund (1992) categorized >75% as eutrophic or hypereutrophic based on their nutrient composition. Similarly, lakes in our study area were naturally eutrophic with elevated levels of TN ($\bar{x}$ = 2199 µg/l) and TP ($\bar{x}$ = 59 µg/l). Accordingly, inputs of fire-derived nutrients must be quite large to produce a detectable and biologically significant increase in lake nutrients. Such inputs will go undetected if they do not exceed background levels of intra- and inter-annual variation, which is sizeable in our study lakes because of the sheer magnitude of their nutrient values. This situation differs from other boreal regions for which fire effects have been previously described. For example, boreal lakes of the Mackenzie River Delta, although located in a similar subarctic habitat, averaged approximately 1000 µg/l of TN and 17 µg/l of TP, both values being less than half our nutrient concentrations (Haszard and Clark 2007). In the Boreal Shield region of Canada, lakes are characteristically poor in nutrients because they are underlain by granitic rock, which is resistant to dissolution (Carignan et al. 2000). Following a forest fire in this region, TP increased 10 µg/l in lakes, representing a 2- to 3-fold increase above pre-fire levels (Carignan et al. 2000); in our study lakes, a 2- to 3-fold increase would require TP inputs of 60–120 µg/l.

While high pre-fire nutrient values tend to dampen the effect of fire-mediated inputs, these values must be considered in combination with the morphology of the surrounding landscape. Notably, our study area has low landscape relief (<10 m) and few, if any, permanent drainage networks on the surface. Lakes in areas of such low relief typically have small catchments, reducing the effective area over which terrestrial nutrients are collected by inflowing

waters (Magnuson et al. 2006). Similarly, catchments of our study lakes, although undefined, are presumably quite small. Supporting this view is the high surface water (15–20% of study area) and lake density (>1.5 lakes per km^2) of our study area, necessitating small catchments, and the generally poor patterns of surface drainage, in which rain and melt water often form pools in localized depressions rather than draining to lakes. Importantly, these small, flat catchments likely restricted erosion and transport of fire-derived nutrients to our lakes, thereby reducing the impact of the fire. In areas with greater topography or larger catchments, effects of fires on lake water chemistry may be more pronounced. For example, a boreal forest fire in mountainous terrain caused 1.5- and 2-fold increases in lake TN and TP, respectively (McEachern et al. 2000). These lakes, because of the variable topography, had clearly defined catchments which were, on average, 21 times greater in area than the actual lakes, a situation clearly different from that of our study area. Indeed, given that nearly 20% of our study area is water, catchments can be, at most, 4 times larger than lake areas (i.e., 80% land / 20% water = 4:1 ratio).

While the restricted flow of small catchments is evident on the surface of our study area, we are unsure of the amount or extent of subsurface flow. If subsurface flow is common, then catchments may be larger than they appear from the surface. Subsurface flow in the Yukon Flats is patchy because of its discontinuous permafrost distribution, being greatest in permafrost-free areas with sand and gravel substrates and reduced or absent in areas with continuous permafrost (Walvoord et al. 2012). Our study area displays a number of landscape features typical of continuous permafrost, including laterally expanding thermokarst lakes, thick deposits of peat on the forest floor, and numerous poorly-drained black spruce bogs (Jorgenson and Osterkamp 2005). Additionally, soils in our study area are dominated by fluvial silts with low hydrologic permeability, further impeding subsurface flow (Williams 1962). Taken together, these

characteristics suggest that subsurface flow is spatially restricted in our study area, if not absent altogether. Thus, as for surface catchments, subsurface catchments are likely small and localized, restricting the spatial extent over which fire-derived nutrients were exported to our lakes.

All of the reasons discussed above – high pre-fire nutrient levels, small catchments, low topography, and permafrost – likely acted in concert to minimize the short-term impact of the fire on water chemistry. Other reasons, although not discussed in detail, may also be important. Fire-derived nutrients may be taken up by soils or vegetation before reaching our lakes. This was documented in Minnesota, in which a large forest fire caused increased phosphorus levels in runoff water, but much of this phosphorus was immobilized in the soil before reaching nearby lakes (McColl and Grigal 1975). Also of importance is the relative magnitude of alternative sources of nutrient inputs, such as snowmelt and precipitation. Bayley et al. (1992) found that post-fire inputs of nitrogen, although elevated, were a minor contributor to lake nutrient budgets in comparison to inputs from precipitation. For our study lakes, precipitation may be an important nutrient input because significant amounts fall directly onto lake surfaces given that nearly 20% of the study area is water. Finally, TP and TN are coarse measurements of a complex nutrient system; other nutrient states, such as dissolved and organic forms, may have been affected by the fire, but masked by our coarse measurements.

Aquatic Invertebrates

Densities of shredders and predators increased in response to the fire, while those of filterers, gatherers, and scrapers did not. We predicted that post-fire increases in invertebrate densities would be driven by fire-mediated nutrient pulses, under the premise that elevated nutrients would stimulate primary productivity, which in turn would increase secondary production of

invertebrates. Because the fire did not increase nutrient levels, other fire-related causes must be responsible for increased shredder and predator densities. While these density increases may not be fire related, we find this unlikely given the strong inference of the BACI study design.

Amphipods accounted for 98% of shredder numbers and were the most numerous invertebrate in our lakes. Scrimgeour et al. (2001) similarly documented increased amphipod numbers in burned lakes, although this was attributed to elevated nutrient levels. Amphipods have high rates of growth and reproduction, often producing ≥5 broods per year, and relatively short life-spans of ± 1 year (Welton and Clarke 1980). Such high rates of reproduction and turnover allow for rapid numerical responses to changing conditions from disturbances such as fires. Rapid density increases were also evident intra-annually, as the year's first bouts of brood production (May–June) led to marked spikes in amphipod densities during our July sampling.

While generally considered shredders, amphipods have a generalist diet that is hard to categorize, including allochthonous and autochthonous plant material and detritus, as well as occasional bouts as predators (MacNeil et al. 1997, Kelly et al. 2002). Generalists often succeed following disturbances such as fires because of their ability to quickly adapt to newly created conditions or habitats. Following a large fire in Yellowstone, trophic generalists were the most abundant invertebrates in streams because of their tolerance of altered physical conditions and resources (Mihuc and Minshall 1995). Similar results were obtained from burnt forests in Idaho, where post-fire streams had greater biomass of r-strategist, generalist invertebrates relative to unburned streams (Malison and Baxter 2010b). For our lakes, fire disturbances included a loss of shade from lakeside canopy cover, loss of shoreline and emergent vegetation, and unidentified changes to water chemistry and resource inputs. These changes, while not quantified, may have favored amphipods and their generalist ecology. Further, our measurement of chlorophyll *a* from

the water column does not account for alternate channels of primary production that may have been affected by the fire, including epibenthic and macrophyte productivity. Macrophytes, in particular, have the potential to influence amphipods because they commonly provide them with both food and refugia from predators (Thiébaut and Gierlinski 2008).

Numbers of predatory aquatic invertebrates also increased in response to the wildfire, the most common of which included Odonata larvae, leeches, and Coleoptera larvae (family Dytiscidae). All of these predators are known to consume amphipods (Merritt et al. 2008). Accordingly, the simplest explanation for their post-fire increase is that the rise in amphipod numbers provided an abundant prey base from which predators could build their populations. This explanation seems plausible when considering the sheer numbers of amphipods in our lakes; amphipods comprised 45% of total invertebrates and their post-fire densities on burned lakes averaged >1000/m^3. Malison and Baxter (2010b) observed similar predator increases in burnt streams, attributing this to an increased prey base of generalist invertebrates that thrived in fire-disturbed habitats. As well, the absence of fish in our lakes reduces predatory pressure on invertebrate predators, potentially allowing their numbers to respond to prey abundance more strongly than in lakes with fish (Bendell and McNicol 1987).

In contrast to shredders and predators, densities of filterers, gatherers, and scrapers were unaffected by the fire. Aquatic invertebrate densities are notoriously variable and, while previous studies have documented fire-mediated changes in their densities, a similar number have found no effect (Rinne 1996, Minshall et al. 1997). The high variability in invertebrate numbers is often ascribed to factors such as season, location, and time, with such factors overriding any potential response to fire (Hochkirch and Adorf 2007). This was the case for filterers, gatherers, and scrapers in our study lakes, as densities of all three groups varied considerably both within and

across years. Moreover, their lack of a fire response was reasonably expected given that nutrient and chlorophyll levels were not affected by the fire. This is especially relevant for filterers and scrapers, which feed directly on the primary production of phytoplankton and epibenthic algae, respectively. Importantly, no negative effects of the fire were detected for any of the five functional feeding groups; densities either increased or did not change in response to the fire.

Waterbird Abundance

Abundance of waterbird young decreased from the pre- to post-fire period, although this decrease was evident on both burned and unburned lakes, suggesting two mutually exclusive interpretations: (1) from the perspective of waterfowl, the fire adversely impacted the entire study area, including burned and unburned lakes, or (2) decreases in chick abundance were independent of the fire and occurred at a spatial scale larger than our study area, thus the concomitant decrease at burned and unburned lakes. Under interpretation 1, a likely mechanism is that fire reduced the amount and quality of nesting habitat in the study site. Waterfowl nest in dense understory vegetation near wetlands (Kantrud 1986), some of which was consumed during the fire. While the loss of these habitats was more severe near burned lakes, waterfowl may choose nesting habitats at scales larger than that of the individual lake, thereby deeming much of the study area as unsuitable following the burn. Indeed, waterfowl often move broods considerable distances from nest to waterbody, suggesting that nesting habitat is chosen at a different scale than that of brood-rearing habitat. Alternatively, interpretation 2 is probable when considering factors that operate on chick abundance at spatial scales large enough to easily encompass our entire study area. Factors include, but are not limited to, temperature, precipitation, predator density, and female breeding propensity. For example, precipitation

during the early brood period lowers chick survival (Krapu et al. 2000). Precipitation occurs at a scale much larger than our study area, such that severe precipitation events would adversely affect chick survival on both burned and unburned lakes, lowering abundance in the process.

Ultimately, while the post-fire decrease in waterbird young may be suggestive of a negative fire impact, we have no definitive evidence of this without a significant interaction between fire and period. This also highlights the strength of the BACI study design – had we conducted solely a post-impact study, as is common in fire research, we would have been unaware that the lower abundance of chicks on burned lakes had existed pre-fire, leading us to falsely conclude that the fire negatively impacted chick abundance. It should also be noted that estimation of abundance for upper-trophic level predators such as waterbirds is inherently difficult due to their small populations and advanced mobility. As such, the high variability associated with our estimate of fire*period may partly reflect this difficulty. Nonetheless, given the high precision of estimates for the remaining parameters in our waterbird models, we think our dataset was sufficient for estimating fire effects, or the lack thereof, on waterbird abundance. Lastly, amphipods are a major prey item of multiple waterbird species, including lesser scaup, which was the most abundant species in our study area (Anteau and Afton 2008). Further, occupancy of lakes by scaup broods is positively related to amphipod density throughout the Yukon Flats (TLL, unpubl. data). Nonetheless, number of waterbird young decreased concurrent with an increase in amphipods on burned lakes. Moreover, chick abundance decreased on unburned lakes as well, even though these lakes experienced no change in amphipod densities. Taken together, these results suggest that chick numbers are responding to other ecological factors operating at large spatial scales, as discussed above, and that smaller scale shifts in amphipod densities are not the primary drivers of chick abundance.

Fire Resilience of Boreal Lakes

The fire in our study area was fairly severe, with 74% of the burn classified as moderate to high severity. Further, because the fire occurred in late summer when permafrost soils were maximally thawed, the burn penetrated deep into the ground and frequently exposed bare mineral soils. Yet, despite this extensive burn, TN and TP did not change in impacted lakes. This stability largely escalated through the trophic structure of our study lakes, as the fire caused little impact in the proceeding trophic levels of primary producers, aquatic invertebrates, and waterbirds. The only exception to this post-fire stability was a positive impact of fire on shredder and predator invertebrates, an observation that warrants further research. For ecologically similar regions of the boreal forest – namely, high aquatic nutrient concentrations and small catchments – these results indicate that, in the short-term, ecosystems of boreal lakes are largely resilient to forest fires. Given the sheer size of the boreal forest in North America (1.5 billion acres) and the number of lakes within its bounds (>2 million), such ecologically similar regions are likely common. The region in which our study occurred, the Yukon Flats, alone has >40,000 lakes and wetlands, many of which are ecologically similar to our study lakes (Heglund 1992). Moreover, our results are especially significant in view of recent changes to fire regimes in the boreal forest. During the 2000s, the annual area of boreal forest burned in Alaska was 50% higher than in any decade since 1940 due to an increased number of years with extensive fires (Kasischke et al. 2010). This increase in fire extent and severity has been linked to climate change in northern latitudes, and climate models indicate a further increase in fire pressure (Chapin et al. 2008). Finally, our results support the belief, put forward by Minshall (2003), that forest fires in general are not detrimental to the sustained maintenance of diverse and productive aquatic ecosystems.

5.6 Acknowledgements

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5.8 Figures

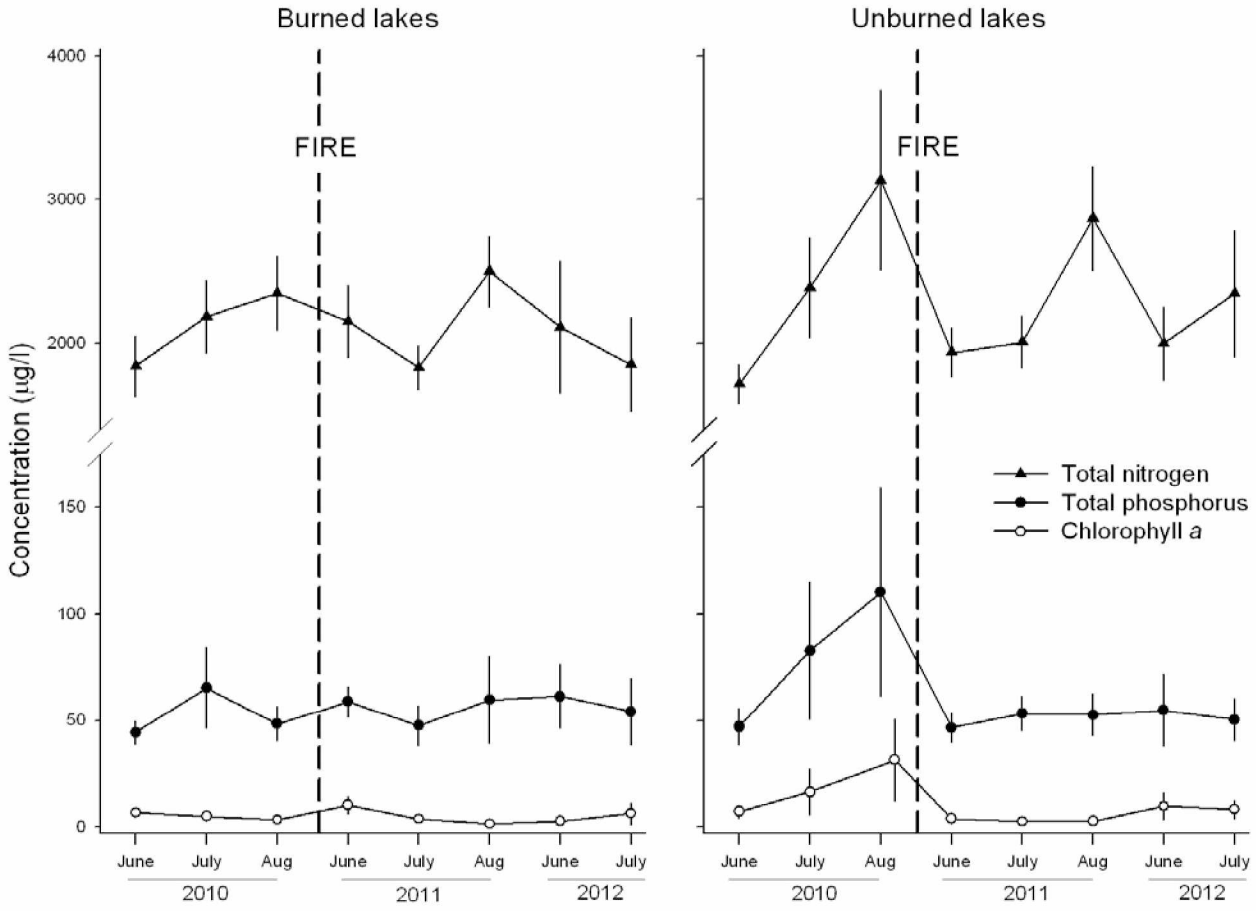

Figure 5-1. Concentrations (µg/l) of total nitrogen, total phosphorus, and chlorophyll *a* from burned and unburned lakes over three consecutive summers (2010–12). The timing of the forest fire is indicated by the dashed vertical line. Concentration values are monthly means ± SEs. Note the break in the scaling of the y-axis.

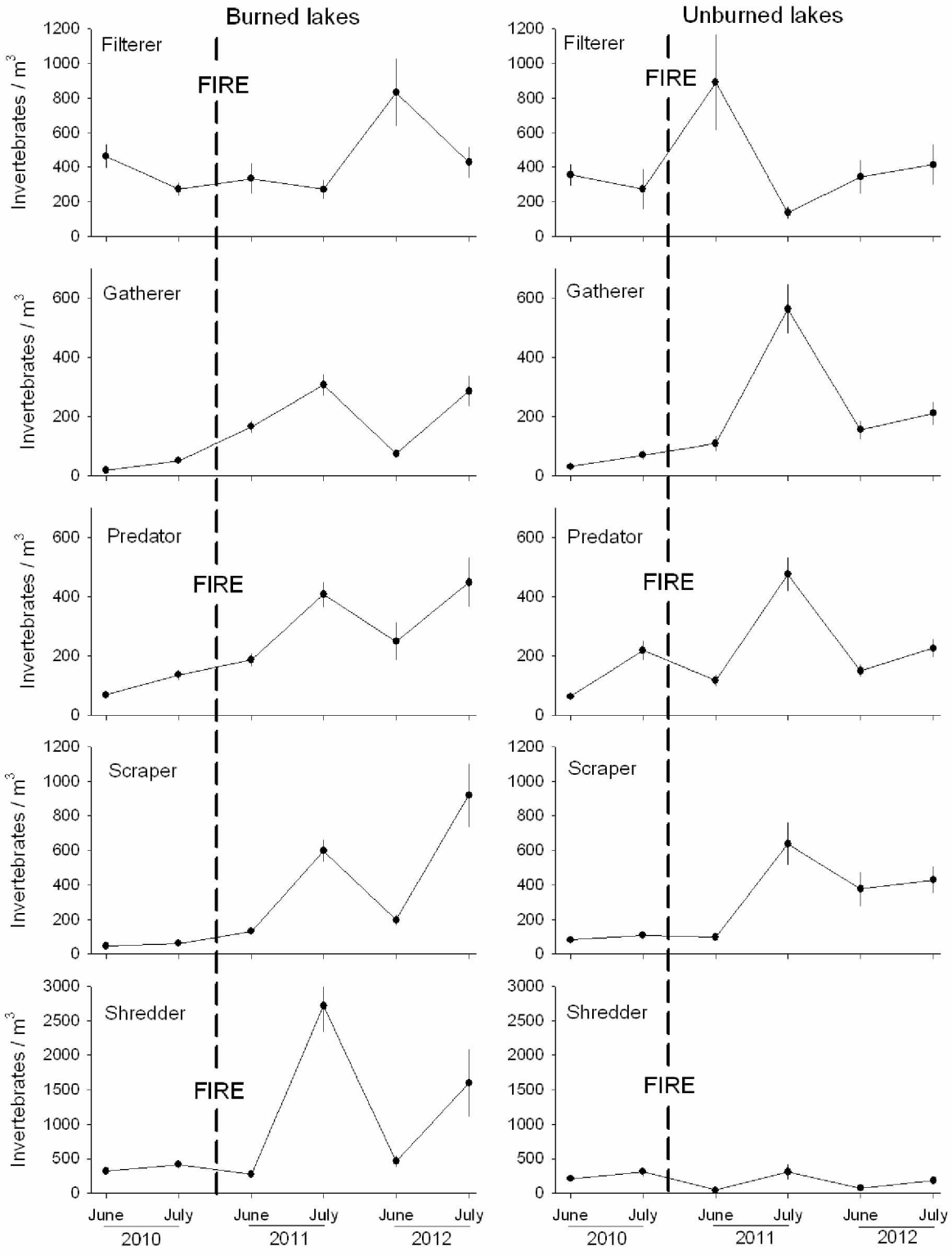

Figure 5-2. Densities (individuals/m^3) of aquatic invertebrates, organized into functional feeding groups, from burned and unburned lakes over three consecutive summers (2010–12). The timing of the forest fire is indicated by the dashed vertical line. Density values are monthly means ± SEs. Note the different scales of the y-axes among functional feeding groups.

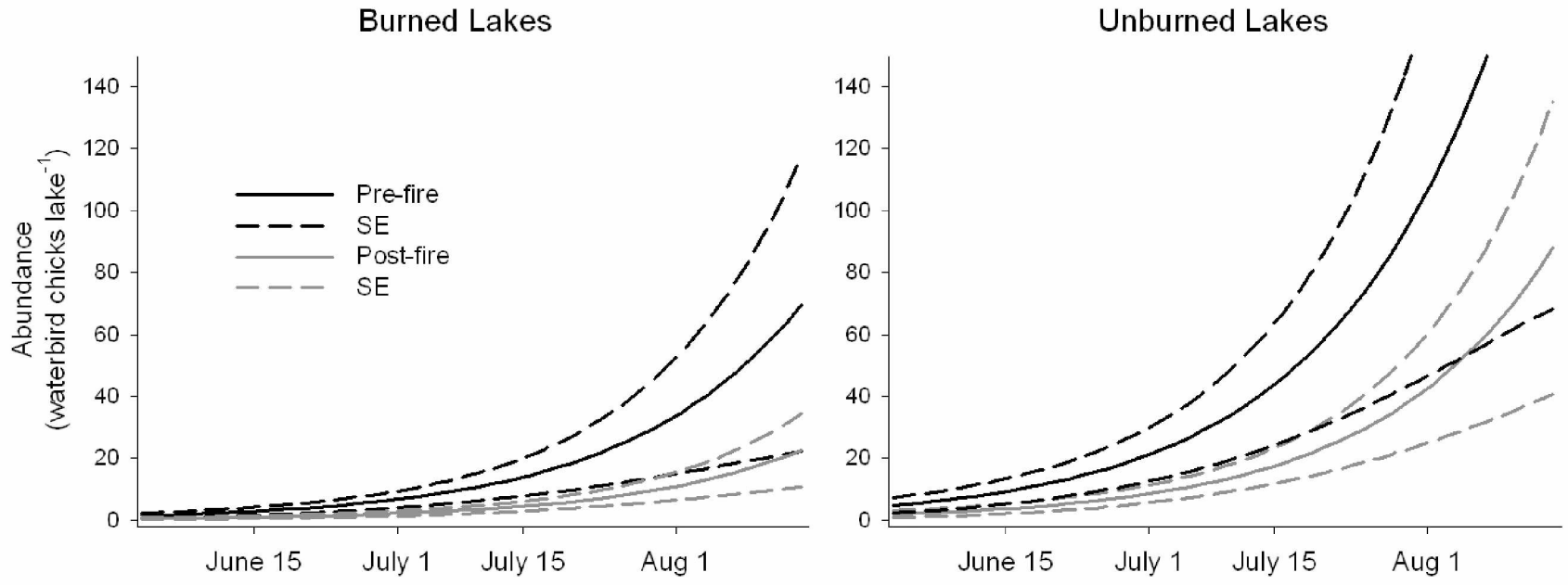

Figure 5-3. N-mixture model results showing the detection-probability corrected relationship between waterbird abundance (chicks/lake) and date. Relationships are categorized by burn category (burned vs. unburned) and period (pre- vs. post-fire).

5.9 Appendix

Appendix 5.A. Supplementary map and images of burned and unburned boreal habitats from our study area.

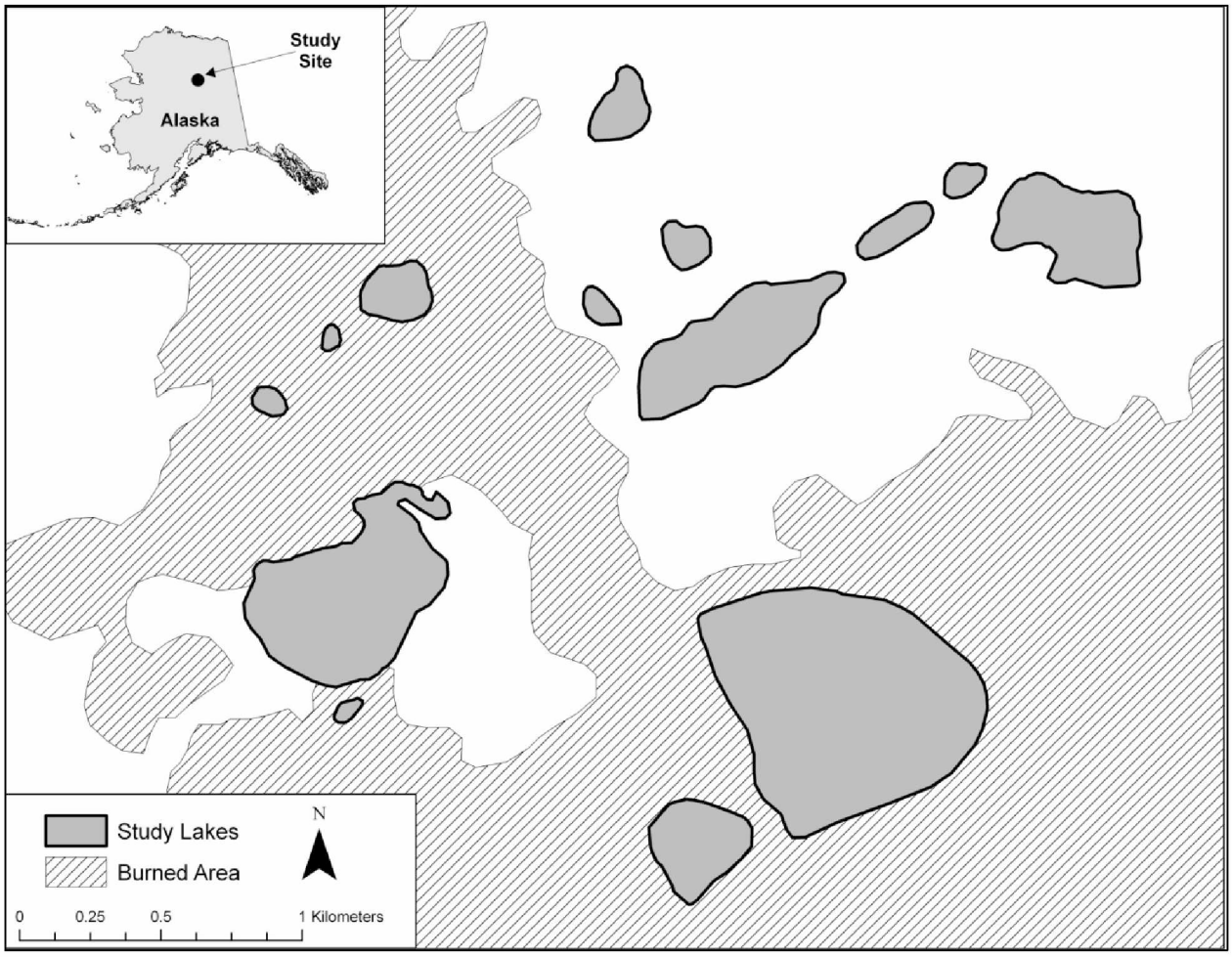

Figure 5.A–1. Map of our study area, located in the Yukon Flats National Wildlife Refuge, Alaska, showing the 14 study lakes and the area impacted by the forest fire.

Figure 5.A–2. Typical boreal forest habitats in our Yukon Flats study area from before and after the wildfire. (A) Burned boreal forest up to the edge of our study lake, with little standing vegetation remaining and peat forest floor removed. (B) Exposed mineral soils near our study lake, resulting from the fire's consumption of the organic soil and peat forest floor. (C) Fire burning in the distance, 3–4 weeks before reaching the study area. Note the dense boreal forest that surrounded the study lakes prior to the fire. (D) Typical unburned boreal forest habitat in our study area. Note the stunted black spruce and peat deposits on the forest floor, both of which are common in permafrost areas. Photo credit: Morgan Pfander (A,B,D) and Mark Lindberg (C).

Appendix 5.B. Model selection results, listed in order of ΔAIC_c, from models evaluating effects of forest fires on water chemistry, aquatic invertebrates, and abundance of waterbird chicks on boreal lakes.

Table 5.B–1. Model selection results for candidate linear mixed models evaluating variation in concentrations of total nitrogen, total phosphorus, and chlorophyll *a* in boreal lakes. Shown are the complete model sets, ranked in order of ΔAIC_c. Model variables include Date (intra-annual date), Year (2010, 2011, 2012), Fire (burned, unburned), Period (pre-, post-fire), and Null (intercept-only model).

Response variable	Model	Parameters	ΔAIC_c	AIC weight (w_i)
Total Nitrogen	Date	5	0	0.69
	Date + Year + Date*Year	9	2.19	0.23
	Date + Fire + Period + Fire*Period	8	5.56	0.04
	Null	4	6.65	0.02
	Year	6	10.33	0
	Fire + Period + Fire*Period	7	12.88	0
Total Phosphorus	Null	4	0	0.49
	Date	5	1.33	0.25
	Year	6	3.25	0.10
	Fire + Period + Fire*Period	7	3.31	0.09
	Date + Fire + Period + Fire*Period	8	4.65	0.05
	Date + Year + Date*Year	9	6.39	0.02
Chlorophyll *a*	Date	5	0	0.48
	Year	6	1.80	0.20
	Null	4	2.38	0.15
	Date + Fire + Period + Fire*Period	8	3.44	0.09
	Date + Year + Date*Year	9	3.99	0.07
	Fire + Period + Fire*Period	7	5.87	0.03

Table 5.B–2. Model selection results for candidate linear mixed models evaluating variation in densities of aquatic invertebrates, organized into functional feeding groups. Shown are the complete model sets, ranked in order of ΔAIC. Model variables include Date (intra-annual date), Year (2010, 2011, 2012), Fire (burned, unburned), Period (pre-, post-fire), and Null (intercept-only model).

Functional Feeding Group	Model	Parameters	ΔAIC	AIC weight (w_i)
Filterer	Date + Year + Date*Year	8	0	0.78
	Date + Fire + Period + Fire*Period	7	2.7	0.20
	Date	4	8.1	0.01
	Year	5	18.4	0
	Fire + Period + Fire*Period	6	19.1	0
	Fire + Period + Fire*Period	3	39.4	0
Gatherer	Date + Year + Date*Year	8	0	1
	Date + Fire + Period + Fire*Period	7	21.2	0
	Year	5	85.6	0
	Fire + Period + Fire*Period	6	95.4	0
	Date	4	274.1	0
	Null	3	395.7	0
Predator	Date + Fire + Period + Fire*Period	7	0	0.76
	Date + Year + Date*Year	8	2.3	0.24
	Date	4	118.9	0
	Fire + Period + Fire*Period	6	127.5	0
	Year	5	140.9	0
	Null	3	306.5	0
Scraper	Date + Year + Date*Year	8	0	0.94
	Date + Fire + Period + Fire*Period	7	5.5	0.06
	Fire + Period + Fire*Period	6	140.7	0
	Year	5	146.5	0
	Date	4	167.0	0
	Null	3	418.4	0

Table 5.B–2 (continued)

Functional Feeding Group	Model	Parameters	ΔAIC	AIC weight (w_i)
Shredder	Date + Fire + Period + Fire*Period	7	0	1
	Date + Year + Date*Year	8	13.7	0
	Date	4	31.0	0
	Fire + Period + Fire*Period	6	127.5	0
	Year	5	163.8	0
	Null	3	166.9	0

Table 5.B–3. N-mixture model selection results for hierarchical generalized linear models evaluating variation in abundance of waterbird chicks (λ) and detection probability (*p*). Shown is the complete model set, ranked in order of ΔAIC_c. Model variables include Area (lake surface area), Date (intra-annual date), Year (2010, 2011, 2012), Fire (burned, unburned), Period (pre-, post-fire), Observer (experienced, inexperienced), and Null (intercept-only model).

Model	Parameters	ΔAIC_c	AIC weight (w_i)
λ(Area + Date + Fire + Period + Fire*Period) *p*(Observer)	9	0	0.94
λ(Area + Date + Year + Date*Year) *p*(Observer)	10	5.60	0.06
λ(Area + Date) *p*(Observer)	6	9.56	0
λ(Area + Fire + Period + Fire*Period) *p*(Observer)	8	16.75	0
λ(Area) *p*(Observer)	5	21.63	0
λ(Area + Year) *p*(Observer)	7	23.91	0
λ(Null) *p*(Null)	3	40.00	0

Appendix 5.C. Parameter estimates and standard errors from models evaluating effects of forest fires on water chemistry, aquatic invertebrates, and abundance of waterbird chicks on boreal lakes.

Table 5.C–1. Model-averaged parameter estimates (Est.) and unconditional standard errors (SE) from linear mixed models evaluating variation in concentrations of total nitrogen, total phosphorus, and chlorophyll *a* in boreal lakes. Estimates are on the log scale. Model variables include Date (intra-annual date), Year (2010, 2011, 2012), Fire (burned, unburned), and Period (pre-, post-fire).

	Total Nitrogen		Total Phosphorus		Chlorophyll *a*	
Parameter	Est.	SE	Est.	SE	Est.	SE
Intercept	6.68	0.29	3.81	0.24	2.36	0.99
Date	0.005	0.001	0.001	0.002	-0.008	0.004
Fire	0.06	0.14	-0.04	0.24	-0.19	0.42
Period	0.04	0.07	-0.03	0.09	0.01	0.26
Fire*Period	0.01	0.08	-0.05	0.44	0.49	0.37
Year 2011	0.22	0.33	0.08	0.38	-0.21	0.87
Year 2012	1.07	0.56	0.09	0.53	0.38	1.43
Date*Year 2011	-0.001	0.002	-0.004	0.002	-0.004	0.008
Date*Year 2012	-0.006	0.003	-0.005	0.005	-0.008	0.014

Reference values for categorical parameters: Fire – unburned; Period – pre-fire; Fire*Period – unburned*pre-fire; Year – 2010; Date*Year – Date*2010.

Table 5.C–2. Parameter estimates (Est.) and standard errors (SE) from linear mixed models evaluating variation in densities of aquatic invertebrates, organized into functional feeding groups. Estimates and SE are derived from the highest ranked model in which the parameter occurred and are on the log scale. Model variables include Date (intra-annual date), Year (2010, 2011, 2012), Fire (burned, unburned), and Period (pre-, post-fire).

	Filterer		Gatherer		Predator		Scraper		Shredder	
Parameter	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Intercept	4.91	1.25	-6.95	1.11	-3.09	0.49	-4.21	1.07	-4.77	0.74
Date	-0.011	0.007	0.40	0.006	0.031	0.002	0.028	0.006	0.041	0.003
Fire	-0.52	0.52	0.01	0.35	-0.36	0.14	-0.06	0.32	-1.88	0.50
Period	0.41	0.13	-2.03	0.12	-1.02	0.09	-1.58	0.12	-0.12	0.15
Fire*Period	-0.42	0.27	0.37	0.24	0.53	0.18	0.45	0.23	1.37	0.27
Year 2011	1.25	1.65	4.61	1.39	2.77	1.08	3.04	1.38	-6.14	1.37
Year 2012	2.72	1.85	3.10	1.67	4.53	1.28	-0.03	1.61	-1.46	1.66
Date*Year 2011	-0.010	0.009	-0.014	0.008	-0.010	0.006	0.025	0.008	0.033	0.008
Date*Year 2012	-0.016	0.010	-0.009	0.009	-0.021	0.007	0.009	0.009	0.007	0.009

Reference values for categorical parameters: Fire – unburned; Period – pre-fire; Fire*Period – unburned*pre-fire; Year – 2010; Date*Year – Date*2010.

Table 5.C–3. Parameter estimates (Est.) and standard errors (SE) from N-mixture models evaluating variation in abundance of waterbird chicks (λ) and detection probability (*p*). Estimates and SE are derived from the highest ranked model in which the parameter occurred and are on the log-scale for abundance parameters and logit-scale for detection probability parameters. Model variables include Area (lake surface area), Date (intra-annual date), Year (2010, 2011, 2012), Fire (burned, unburned), Period (pre-, post-fire), and Observer (experienced, inexperienced).

Parameter	Estimate	SE
λ Intercept	1.06	0.36
Area	1.29	0.25
Date	1.13	0.26
Fire	1.36	0.48
Period	1.12	0.55
Fire*Period	-0.21	0.73
Year 2011	-0.74	0.42
Year 2012	-1.55	0.54
Date*Year 2011	-0.15	0.52
Date*Year 2012	1.97	0.78
p Intercept	0.05	0.10
Observer[f]	0.15	0.09

Reference values for categorical parameters: Fire – unburned; Period – pre-fire; Fire*Period – unburned*pre-fire; Year – 2010; Date*Year – Date*2010; Observer – experienced.

Chapter 6

General Conclusions

This dissertation provides the first known examination of how ecosystems of Subarctic boreal lakes respond to increasing environmental stressors caused by climate warming. From primary producers to top predators, lake ecosystems displayed an unforeseen resilience to (1) rising chemical concentrations associated with long-term losses in surface area, and (2) a large wildfire that removed large stands of boreal forest.

Waterbirds are the top predators on Subarctic boreal lakes of the Yukon Flats during the summer breeding season (Heglund, 1992, Corcoran et al. 2009), feeding primarily on aquatic invertebrates. In Chapter 2, I found that occupancy and species richness of waterbird broods were strongly and positively related to amphipod density, while having no relation to density of other common macroinvertebrates. Species richness increased 5-fold across the range of observed amphipod densities, from 2–3 to >15 waterbird species. Similarly, 3 water chemistry covariates (total nitrogen, total phosphorus, and chlorophyll *a* concentrations), each of which provides an index of lake productivity, were positively related to species richness; however, waterbird occupancy rates were largely unrelated to water chemistry. Finally, nesting habitats had no influence on species richness and occupancy, suggesting that distributions and diversity of waterbird broods are driven by the presence of quality brood-rearing lakes, not nesting sites. Overall, my findings highlight the main environmental drivers of waterbird distributions and diversity, providing a framework for understanding impacts of long-term habitat changes on breeding waterbird populations of the Yukon Flats.

Losses in lake area have been observed for several Arctic and Subarctic regions in recent decades (Carroll et al. 2011, Rover et al. 2012). These reductions are thought to be driven by increased evaporation and accelerated permafrost degradation, both of which may cause concurrent changes to lake water chemistry (Smol and Douglas 2007). For chapter 3 I made use of an historic database of past lake conditions, finding that concentrations of 2 nutrients (total nitrogen, total phosphorus) and 4 ions (calcium, chloride, magnesium, sodium) increased in shrinking lakes from 1985–1989 to 2010–2012 while simultaneously undergoing little change on stable lakes. Moreover, concentration increases in shrinking lakes were of a substantial magnitude, including increases of >500% for chloride, >200% for total nitrogen, and >100% for total phosphorus. An imbalanced evaporation-to-inflow ratio appeared to be a major driver of such chemical changes, whereby evaporative water losses concentrated solutes into smaller water volumes.

Building on the results of the previous chapter, I examined the impacts of chemical changes on trophic dynamics of Subarctic boreal lakes in Chapter 4. In particular, the elevated nutrient concentrations may increase primary productivity, which may then transfer upward to higher trophic levels (Peterson et al. 1993, Slavik et al. 2004). At the base of the food web, I found that phytoplankton stocks, as indexed by chlorophyll concentrations, remained largely unchanged on both shrinking and stable lakes from 1985–1989 to 2010–2012. Further up the trophic chain, I found large changes in invertebrate abundance over time, including decreased abundance of 5 of the 6 groups we examined: Amphipoda, Coleoptera, Corixidae, Gastropoda, and Odonata. These decadal changes, however, were not limited to shrinking lakes, occurring on lakes with stable surface areas as well. Finally, at the top of the food web, I observed that lake occupancy rates of waterbirds, including adults and chicks, remained largely unchanged from

1985–1989 to 2010–2012. These collective results suggest that lake ecosystems have been, to date, largely resilient to chemical changes on shrinking lakes.

In addition to losses in surface area, fires may also impact lake water chemistry by releasing terrestrial nutrients and organic matter that may be transported to nearby lakes (Carnignan et al. 2000, McEachern et al. 2000). Following a severe fire at one my study sites, I found that concentrations of total nitrogen and phosphorus remained unchanged from the pre-fire period. Likewise, chlorophyll a levels were unaffected by the fire, likely reflecting the stable nutrient concentrations from pre- to post-fire. For aquatic invertebrates, I found that densities of three functional feeding groups did not respond to the fire (filterers, gatherers, scrapers), while two groups increased (shredders, predators). Lastly, abundance of waterbird chicks, which feed primarily on aquatic invertebrates, were unaffected by the fire. Overall, our results indicate that fire was not detrimental to the sustained maintenance of lake ecosystems in the short-term. This was likely due, in part, to their remarkably high initial nutrient concentrations, which acted to dampen the impact nutrient inputs from the fire.

In summary, lakes of the Yukon Flats are exposed to several environmental stressors that have been exacerbated by recent climatic warming. Foremost, increased evaporative water losses have caused 9–16% of lakes in the region to lose significant surface area (Rover et al. 2012), which in turn caused pronounced increases in aquatic nutrient and ion concentrations. At the same time, forest fires in the boreal forest have become more frequent and more severe (Kelly et al. 2013), and these fires may impact the abundant lakes found throughout the region. Nonetheless, ecosystems of Yukon Flats lakes have proven largely resilient to such stressors to date. Moreover, this resilience spanned multiple trophic levels, from phytoplankton to aquatic invertebrates to waterbirds. This apparent resilience, however, cannot be reliably extrapolated

into the future, primarily owing to sustained climatic warming that may further exacerbate drying of lakes and burning of forests. Often, lake ecosystems exhibit an impressive degree of resilience up to some threshold, after which they undergo abrupt changes to alternative states (Carpenter 2003). For our study lakes, and lakes of similar Arctic and Subarctic regions, this hypothetic threshold may be quickly approaching given the high magnitude of chemical changes and losses on invertebrate abundance that have already occurred.

6.1 References

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Appendix

Appendix A. Mean (± standard error) limnological characteristics of lakes of the Yukon Flats, Alaska, across two time periods: 1985–1989 versus 2010–2012.

Lake	Limnological characteristic	1985–1989	2010–2012
C 4	Total nitrogen (µg/l)	547.50 ± 60.19	1618.75 ± 51.53
	Total phosphorus (µg/l)	57.25 ± 5.22	31.63 ± 0.75
	Calcium (mg/l)	47.78 ± 2.77	43.33 ± 6.21
	Sodium (mg/l)	4.40 ± 0.33	15.08 ± 0.60
	Magnesium (mg/l)	10.56 ± 1.26	22.89 ± 0.31
	Potassium (mg/l)	3.01 ± 2.16	0.63 ± 0.20
	Chloride (mg/l)	1.33 ± 0.12	9.20 ± 0.27
	Sulfate (mg/l)	5.16 ± 0.50	20.58 ± 3.50
	Chlorophyll (µg/l)	11.33 ± 4.43	1.70 ± 0.23
	Non-volatile suspended solids (mg/l)	0.65 ± 0.31	0.18 ± 0.06
	Volatile suspended solids (mg/l)	2.15 ± 0.46	0.68 ± 0.09
	Total suspended solids (mg/l)	2.80 ± 0.66	0.85 ± 0.06
	Conductivity (µS/mol)	296.67 ± 20.20	397.75 ± 29.37
	pH	8.13 ± 0.13	9.04 ± 0.24
	Temperature (° C)	17.25 ± 1.49	19.75 ± 1.18
C 6	Total nitrogen (µg/l)	865.00 ± 251.86	2038.75 ± 196.86
	Total phosphorus (µg/l)	94.50 ± 13.76	31.38 ± 1.93
	Calcium (mg/l)	49.47 ± 5.51	44.11 ± 5.24
	Sodium (mg/l)	4.68 ± 0.14	10.41 ± 0.75
	Magnesium (mg/l)	13.81 ± 0.91	20.91 ± 0.79
	Potassium (mg/l)	0.95 ± 0.17	2.28 ± 0.36
	Chloride (mg/l)	2.00 ± 0.29	7.78 ± 0.55
	Sulfate (mg/l)	5.91 ± 0.97	0.63 ± 0.42
	Chlorophyll (µg/l)	31.55 ± 8.43	2.96 ± 0.40
	Non-volatile suspended solids (mg/l)	1.18 ± 0.52	0.43 ± 0.10
	Volatile suspended solids (mg/l)	7.75 ± 1.95	1.48 ± 0.27

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 6	Total suspended solids (mg/l)	8.93 ± 2.39	1.90 ± 0.31
	Conductivity (µS/mol)	322.80 ± 31.55	354.75 ± 27.33
	pH	8.25 ± 0.17	8.78 ± 0.19
	Temperature (° C)	18.40 ± 1.96	19.21 ± 0.97
C 7	Total nitrogen (µg/l)	804.29 ± 265.81	1612.50 ± 70.78
	Total phosphorus (µg/l)	34.57 ± 2.94	33.00 ± 2.07
	Calcium (mg/l)	42.18 ± 5.23	61.96 ± 3.56
	Sodium (mg/l)	4.28 ± 0.17	13.54 ± 0.46
	Magnesium (mg/l)	12.90 ± 0.54	21.65 ± 0.76
	Potassium (mg/l)	0.46 ± 0.16	0.79 ± 0.29
	Chloride (mg/l)	1.25 ± 0.14	8.51 ± 0.20
	Sulfate (mg/l)	3.03 ± 0.70	0.00 ± 0.00
	Chlorophyll (µg/l)	3.04 ± 0.84	3.23 ± 0.36
	Non-volatile suspended solids (mg/l)	0.31 ± 0.21	0.29 ± 0.06
	Volatile suspended solids (mg/l)	1.51 ± 0.30	1.01 ± 0.09
	Total suspended solids (mg/l)	1.83 ± 0.44	1.30 ± 0.13
	Conductivity (µS/mol)	274.33 ± 29.35	448.75 ± 17.94
	pH	8.50 ± 0.33	8.33 ± 0.15
	Temperature (° C)	16.00 ± 1.57	19.26 ± 1.07
C 8	Total nitrogen (µg/l)	1062.86 ± 325.29	2251.25 ± 193.18
	Total phosphorus (µg/l)	53.71 ± 4.26	45.75 ± 2.90
	Calcium (mg/l)	48.95 ± 7.16	56.60 ± 9.69
	Sodium (mg/l)	7.22 ± 0.82	21.49 ± 1.53
	Magnesium (mg/l)	16.49 ± 0.86	29.55 ± 0.73
	Potassium (mg/l)	1.95 ± 1.28	0.20 ± 0.09
	Chloride (mg/l)	1.75 ± 0.14	15.16 ± 1.44
	Sulfate (mg/l)	7.76 ± 1.28	56.65 ± 13.75
	Chlorophyll (µg/l)	9.33 ± 1.19	4.83 ± 0.73

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 8	Non-volatile suspended solids (mg/l)	1.17 ± 0.62	0.60 ± 0.19
	Volatile suspended solids (mg/l)	3.96 ± 1.00	1.46 ± 0.16
	Total suspended solids (mg/l)	5.13 ± 1.60	2.06 ± 0.33
	Conductivity (µS/mol)	318.00 ± 38.57	503.13 ± 47.26
	pH	8.76 ± 0.37	9.10 ± 0.25
	Temperature (° C)	15.83 ± 1.82	19.26 ± 1.42
C 9	Total nitrogen (µg/l)	1174.00 ± 311.31	3140.00 ± 314.78
	Total phosphorus (µg/l)	94.14 ± 17.06	116.25 ± 22.47
	Calcium (mg/l)	37.41 ± 3.58	31.38 ± 3.12
	Sodium (mg/l)	7.34 ± 0.44	15.01 ± 1.20
	Magnesium (mg/l)	17.03 ± 0.50	19.80 ± 1.05
	Potassium (mg/l)	0.46 ± 0.17	5.08 ± 0.69
	Chloride (mg/l)	1.75 ± 0.14	10.81 ± 0.88
	Sulfate (mg/l)	4.61 ± 0.97	0.00 ± 0.00
	Chlorophyll (µg/l)	12.70 ± 5.64	29.03 ± 14.37
	Non-volatile suspended solids (mg/l)	0.67 ± 0.44	0.99 ± 0.22
	Volatile suspended solids (mg/l)	4.13 ± 1.78	5.03 ± 1.42
	Total suspended solids (mg/l)	4.80 ± 1.84	6.01 ± 1.54
	Conductivity (µS/mol)	285.00 ± 18.26	313.63 ± 26.11
	pH	9.00 ± 0.24	9.81 ± 0.21
	Temperature (° C)	16.50 ± 1.88	18.94 ± 1.31
C 10	Total nitrogen (µg/l)	1248.57 ± 433.08	3121.25 ± 533.59
	Total phosphorus (µg/l)	149.86 ± 30.10	123.63 ± 40.18
	Calcium (mg/l)	36.30 ± 1.69	30.59 ± 4.59
	Sodium (mg/l)	6.41 ± 0.39	10.58 ± 1.15
	Magnesium (mg/l)	13.67 ± 0.86	17.05 ± 0.65
	Potassium (mg/l)	3.98 ± 0.22	6.18 ± 0.52
	Chloride (mg/l)	1.95 ± 0.32	7.16 ± 0.65

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 10	Sulfate (mg/l)	1.99 ± 0.48	0.00 ± 0.00
	Chlorophyll (µg/l)	31.07 ± 11.09	33.88 ± 15.37
	Non-volatile suspended solids (mg/l)	3.51 ± 1.28	2.05 ± 1.02
	Volatile suspended solids (mg/l)	19.46 ± 5.95	20.75 ± 10.63
	Total suspended solids (mg/l)	22.97 ± 6.93	22.80 ± 11.30
	Conductivity (µS/mol)	279.50 ± 11.88	288.00 ± 28.37
	pH	8.90 ± 0.19	9.46 ± 0.27
	Temperature (° C)	16.83 ± 1.90	19.64 ± 1.05
C 11	Total nitrogen (µg/l)	1095.71 ± 343.70	1890.00 ± 174.25
	Total phosphorus (µg/l)	58.00 ± 12.00	39.00 ± 2.43
	Calcium (mg/l)	35.62 ± 6.48	40.08 ± 5.53
	Sodium (mg/l)	6.04 ± 0.34	14.41 ± 0.72
	Magnesium (mg/l)	15.04 ± 0.90	22.80 ± 0.58
	Potassium (mg/l)	0.59 ± 0.22	0.89 ± 0.24
	Chloride (mg/l)	1.63 ± 0.24	9.11 ± 0.53
	Sulfate (mg/l)	4.87 ± 0.75	15.23 ± 4.70
	Chlorophyll (µg/l)	13.04 ± 7.99	2.85 ± 0.32
	Non-volatile suspended solids (mg/l)	0.24 ± 0.07	0.75 ± 0.25
	Volatile suspended solids (mg/l)	1.87 ± 0.36	1.60 ± 0.35
	Total suspended solids (mg/l)	2.11 ± 0.36	2.35 ± 0.57
	Conductivity (µS/mol)	249.80 ± 22.87	367.25 ± 28.47
	pH	9.19 ± 0.36	9.20 ± 0.27
	Temperature (° C)	15.17 ± 1.82	18.69 ± 0.71
C 12	Total nitrogen (µg/l)	976.67 ± 176.08	1361.25 ± 74.94
	Total phosphorus (µg/l)	70.43 ± 24.94	36.75 ± 4.50
	Calcium (mg/l)	55.67 ± 1.83	38.64 ± 2.56
	Sodium (mg/l)	4.34 ± 0.21	4.25 ± 0.32
	Magnesium (mg/l)	14.67 ± 0.96	11.06 ± 0.54

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 12	Potassium (mg/l)	0.88 ± 0.38	0.98 ± 0.31
	Chloride (mg/l)	1.70 ± 0.12	2.27 ± 0.16
	Sulfate (mg/l)	1.93 ± 0.54	0.00 ± 0.00
	Chlorophyll (µg/l)	12.10 ± 3.49	7.99 ± 2.19
	Non-volatile suspended solids (mg/l)	0.96 ± 0.36	0.69 ± 0.12
	Volatile suspended solids (mg/l)	3.11 ± 0.60	2.23 ± 0.46
	Total suspended solids (mg/l)	4.07 ± 0.86	2.91 ± 0.57
	Conductivity (µS/mol)	331.50 ± 14.83	243.25 ± 14.47
	pH	7.86 ± 0.08	8.65 ± 0.23
	Temperature (° C)	17.33 ± 1.58	19.71 ± 0.94
C 13	Total nitrogen (µg/l)	903.33 ± 139.35	2295.00 ± 133.87
	Total phosphorus (µg/l)	59.86 ± 5.38	37.38 ± 2.21
	Calcium (mg/l)	42.01 ± 2.27	60.85 ± 1.36
	Sodium (mg/l)	4.56 ± 0.25	7.15 ± 0.38
	Magnesium (mg/l)	13.08 ± 1.01	21.50 ± 0.88
	Potassium (mg/l)	2.93 ± 0.15	2.31 ± 0.22
	Chloride (mg/l)	1.88 ± 0.38	5.16 ± 0.33
	Sulfate (mg/l)	3.58 ± 0.35	2.25 ± 1.49
	Chlorophyll (µg/l)	14.34 ± 4.04	2.51 ± 0.47
	Non-volatile suspended solids (mg/l)	1.70 ± 1.08	0.49 ± 0.23
	Volatile suspended solids (mg/l)	6.44 ± 2.85	1.78 ± 0.35
	Total suspended solids (mg/l)	8.14 ± 3.91	2.26 ± 0.56
	Conductivity (µS/mol)	273.67 ± 18.29	357.25 ± 43.77
	pH	8.01 ± 0.06	7.83 ± 0.27
	Temperature (° C)	17.71 ± 1.80	20.68 ± 1.04
C 16	Total nitrogen (µg/l)	1390.00 ± 395.19	1715.00 ± 87.03
	Total phosphorus (µg/l)	78.43 ± 8.56	50.38 ± 4.11
	Calcium (mg/l)	38.00 ± 2.20	35.66 ± 3.16

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 16	Sodium (mg/l)	5.32 ± 0.35	10.29 ± 0.51
	Magnesium (mg/l)	12.19 ± 0.91	18.65 ± 0.35
	Potassium (mg/l)	2.01 ± 0.22	2.59 ± 0.37
	Chloride (mg/l)	1.75 ± 0.14	5.90 ± 0.36
	Sulfate (mg/l)	3.74 ± 0.53	6.63 ± 3.40
	Chlorophyll (µg/l)	22.90 ± 14.31	8.83 ± 2.12
	Non-volatile suspended solids (mg/l)	1.36 ± 0.77	0.65 ± 0.15
	Volatile suspended solids (mg/l)	5.21 ± 1.81	2.46 ± 0.57
	Total suspended solids (mg/l)	6.57 ± 1.87	3.11 ± 0.71
	Conductivity (µS/mol)	244.83 ± 16.99	315.75 ± 17.87
	pH	8.21 ± 0.24	8.64 ± 0.09
	Temperature (° C)	16.57 ± 1.17	17.86 ± 0.89
C 18	Total nitrogen (µg/l)	650.00 ± 159.19	3011.76 ± 163.77
	Total phosphorus (µg/l)	76.00 ± 8.60	133.88 ± 11.53
	Calcium (mg/l)	32.23 ± 4.18	29.84 ± 1.85
	Sodium (mg/l)	5.72 ± 0.45	12.42 ± 1.93
	Magnesium (mg/l)	10.30 ± 1.41	18.39 ± 0.50
	Potassium (mg/l)	3.83 ± 0.63	8.00 ± 0.58
	Chloride (mg/l)	2.00 ± 0.20	5.18 ± 0.12
	Sulfate (mg/l)	1.96 ± 0.33	26.24 ± 7.11
	Chlorophyll (µg/l)	12.06 ± 3.05	39.40 ± 19.21
	Non-volatile suspended solids (mg/l)	0.59 ± 0.63	2.51 ± 0.66
	Volatile suspended solids (mg/l)	4.73 ± 1.07	7.33 ± 1.83
	Total suspended solids (mg/l)	5.31 ± 1.18	9.84 ± 2.30
	Conductivity (µS/mol)	237.33 ± 25.89	287.47 ± 15.81
	pH	9.07 ± 0.30	9.94 ± 0.14
	Temperature (° C)	17.71 ± 1.32	19.16 ± 0.66
C 19	Total nitrogen (µg/l)	748.57 ± 169.26	1596.25 ± 57.69

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 19	Total phosphorus (µg/l)	66.57 ± 8.63	43.00 ± 2.45
	Calcium (mg/l)	40.18 ± 1.62	40.38 ± 2.05
	Sodium (mg/l)	6.45 ± 0.19	9.89 ± 0.35
	Magnesium (mg/l)	13.65 ± 0.66	17.35 ± 0.40
	Potassium (mg/l)	2.00 ± 0.50	1.99 ± 0.48
	Chloride (mg/l)	2.13 ± 0.13	5.06 ± 0.24
	Sulfate (mg/l)	1.80 ± 0.19	3.25 ± 2.20
	Chlorophyll (µg/l)	7.63 ± 1.43	3.99 ± 0.90
	Non-volatile suspended solids (mg/l)	0.26 ± 0.11	0.29 ± 0.09
	Volatile suspended solids (mg/l)	2.13 ± 0.42	1.41 ± 0.35
	Total suspended solids (mg/l)	2.39 ± 0.49	1.70 ± 0.43
	Conductivity (µS/mol)	274.17 ± 5.89	318.38 ± 15.73
	pH	7.94 ± 0.09	8.46 ± 0.14
	Temperature (° C)	16.71 ± 1.36	18.68 ± 0.80
C 22	Total nitrogen (µg/l)	1182.86 ± 417.87	2619.41 ± 147.16
	Total phosphorus (µg/l)	85.14 ± 24.16	56.82 ± 2.85
	Calcium (mg/l)	38.61 ± 2.64	35.56 ± 2.34
	Sodium (mg/l)	4.96 ± 0.26	6.53 ± 0.26
	Magnesium (mg/l)	9.11 ± 0.77	15.08 ± 1.04
	Potassium (mg/l)	4.04 ± 0.51	7.37 ± 1.26
	Chloride (mg/l)	1.25 ± 0.14	2.49 ± 0.29
	Sulfate (mg/l)	1.93 ± 0.22	21.06 ± 6.46
	Chlorophyll (µg/l)	17.29 ± 9.94	6.10 ± 1.20
	Non-volatile suspended solids (mg/l)	0.64 ± 0.48	0.59 ± 0.09
	Volatile suspended solids (mg/l)	4.24 ± 1.92	2.22 ± 0.37
	Total suspended solids (mg/l)	4.89 ± 2.37	2.82 ± 0.43
	Conductivity (µS/mol)	214.33 ± 19.02	263.53 ± 19.78
	pH	8.59 ± 0.26	9.78 ± 0.13

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
C 22	Temperature (° C)	16.86 ± 1.08	19.69 ± 0.59
C 23	Total nitrogen (µg/l)	935.00 ± 239.69	2452.50 ± 371.28
	Total phosphorus (µg/l)	39.14 ± 3.90	46.75 ± 5.55
	Calcium (mg/l)	24.34 ± 2.41	24.26 ± 1.35
	Sodium (mg/l)	4.24 ± 0.79	6.90 ± 1.05
	Magnesium (mg/l)	9.19 ± 0.70	9.08 ± 0.75
	Potassium (mg/l)	2.00 ± 0.91	2.73 ± 0.88
	Chloride (mg/l)	1.75 ± 0.32	5.37 ± 1.02
	Sulfate (mg/l)	1.58 ± 0.23	5.13 ± 3.39
	Chlorophyll (µg/l)	4.20 ± 1.15	7.58 ± 3.44
	Non-volatile suspended solids (mg/l)	0.57 ± 0.54	0.96 ± 0.37
	Volatile suspended solids (mg/l)	1.99 ± 1.04	3.14 ± 0.74
	Total suspended solids (mg/l)	2.56 ± 1.58	4.10 ± 1.06
	Conductivity (µS/mol)	201.33 ± 16.78	202.86 ± 13.56
	pH	9.26 ± 0.39	9.97 ± 0.21
	Temperature (° C)	17.00 ± 1.93	20.50 ± 1.47
D 1	Total nitrogen (µg/l)	1212.22 ± 147.60	1692.00 ± 87.54
	Total phosphorus (µg/l)	30.67 ± 3.61	26.80 ± 2.11
	Calcium (mg/l)	25.95 ± 1.11	30.84 ± 1.83
	Sodium (mg/l)	11.85 ± 2.92	14.28 ± 0.37
	Magnesium (mg/l)	13.63 ± 1.97	24.52 ± 0.54
	Potassium (mg/l)	9.00 ± 2.47	10.40 ± 0.13
	Chloride (mg/l)	1.67 ± 0.32	5.73 ± 0.09
	Sulfate (mg/l)	0.73 ± 0.27	0.00 ± 0.00
	Chlorophyll (µg/l)	3.71 ± 0.41	4.24 ± 1.00
	Non-volatile suspended solids (mg/l)	0.90 ± 0.34	0.42 ± 0.12
	Volatile suspended solids (mg/l)	0.92 ± 0.17	2.28 ± 0.37
	Total suspended solids (mg/l)	1.82 ± 0.30	2.70 ± 0.33

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 1	Conductivity (µS/mol)	273.67 ± 12.42	305.80 ± 42.60
	pH	8.22 ± 0.17	8.78 ± 0.07
	Temperature (° C)	15.22 ± 1.54	18.88 ± 0.79
D 2	Total nitrogen (µg/l)	1160.00 ± 288.13	1000.00 ± 40.50
	Total phosphorus (µg/l)	69.22 ± 6.46	60.33 ± 7.63
	Calcium (mg/l)	9.08 ± 1.96	17.42 ± 3.28
	Sodium (mg/l)	0.83 ± 0.21	1.00 ± 0.50
	Magnesium (mg/l)	2.72 ± 0.51	6.35 ± 1.24
	Potassium (mg/l)	2.09 ± 0.23	1.93 ± 0.49
	Chloride (mg/l)	1.76 ± 0.57	0.86 ± 0.19
	Sulfate (mg/l)	4.17 ± 0.87	39.95 ± 11.46
	Chlorophyll (µg/l)	15.19 ± 5.75	4.27 ± 1.48
	Non-volatile suspended solids (mg/l)	9.72 ± 5.11	1.35 ± 0.80
	Volatile suspended solids (mg/l)	3.24 ± 0.78	1.65 ± 0.37
	Total suspended solids (mg/l)	12.96 ± 5.70	3.00 ± 1.16
	Conductivity (µS/mol)	70.60 ± 11.50	142.97 ± 27.11
	pH	7.19 ± 0.23	8.93 ± 0.52
	Temperature (° C)	16.20 ± 1.39	18.87 ± 0.89
D 4	Total nitrogen (µg/l)	698.75 ± 160.34	1138.00 ± 89.47
	Total phosphorus (µg/l)	38.00 ± 5.61	35.20 ± 6.71
	Calcium (mg/l)	10.24 ± 1.89	17.84 ± 2.23
	Sodium (mg/l)	1.17 ± 0.16	0.88 ± 0.23
	Magnesium (mg/l)	3.72 ± 0.52	6.78 ± 0.77
	Potassium (mg/l)	1.90 ± 0.33	1.82 ± 0.27
	Chloride (mg/l)	1.27 ± 0.19	1.91 ± 0.14
	Sulfate (mg/l)	2.37 ± 0.65	24.42 ± 6.10
	Chlorophyll (µg/l)	4.29 ± 1.04	4.22 ± 0.88
	Non-volatile suspended solids (mg/l)	1.38 ± 0.47	0.36 ± 0.21

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 4	Volatile suspended solids (mg/l)	1.07 ± 0.28	1.08 ± 0.24
	Total suspended solids (mg/l)	2.45 ± 0.56	1.44 ± 0.41
	Conductivity (µS/mol)	81.20 ± 11.25	130.20 ± 19.17
	pH	6.94 ± 0.14	7.16 ± 0.21
	Temperature (° C)	14.70 ± 1.32	20.50 ± 1.14
D 6	Total nitrogen (µg/l)	883.33 ± 202.64	1336.67 ± 149.57
	Total phosphorus (µg/l)	37.22 ± 3.11	40.17 ± 9.05
	Calcium (mg/l)	16.06 ± 2.18	13.80 ± 1.41
	Sodium (mg/l)	2.26 ± 0.17	2.42 ± 0.22
	Magnesium (mg/l)	6.11 ± 0.64	5.62 ± 0.52
	Potassium (mg/l)	2.36 ± 0.26	2.88 ± 0.72
	Chloride (mg/l)	1.47 ± 0.29	2.17 ± 0.34
	Sulfate (mg/l)	2.00 ± 0.60	0.00 ± 0.00
	Chlorophyll (µg/l)	2.91 ± 0.64	3.20 ± 0.84
	Non-volatile suspended solids (mg/l)	1.46 ± 0.35	0.57 ± 0.22
	Volatile suspended solids (mg/l)	1.67 ± 0.28	2.37 ± 0.75
	Total suspended solids (mg/l)	3.13 ± 0.49	2.93 ± 0.95
	Conductivity (µS/mol)	132.80 ± 14.96	112.73 ± 5.76
	pH	6.43 ± 0.05	6.64 ± 0.28
	Temperature (° C)	13.30 ± 1.32	18.10 ± 0.89
D 7	Total nitrogen (µg/l)	855.56 ± 224.72	1500.00 ± 83.86
	Total phosphorus (µg/l)	40.75 ± 6.52	50.00 ± 3.88
	Calcium (mg/l)	19.26 ± 1.46	25.42 ± 1.22
	Sodium (mg/l)	2.55 ± 0.10	2.65 ± 0.19
	Magnesium (mg/l)	7.35 ± 0.63	11.87 ± 1.03
	Potassium (mg/l)	2.53 ± 0.12	1.45 ± 0.59
	Chloride (mg/l)	1.24 ± 0.25	1.67 ± 0.30
	Sulfate (mg/l)	1.31 ± 0.53	3.17 ± 2.10

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 7	Chlorophyll (µg/l)	4.10 ± 0.82	5.45 ± 0.98
	Non-volatile suspended solids (mg/l)	1.75 ± 0.76	2.92 ± 1.55
	Volatile suspended solids (mg/l)	1.24 ± 0.28	2.80 ± 0.70
	Total suspended solids (mg/l)	2.99 ± 0.86	5.72 ± 1.81
	Conductivity (µS/mol)	153.40 ± 8.17	198.92 ± 28.85
	pH	6.92 ± 0.12	8.41 ± 0.32
	Temperature (° C)	15.00 ± 1.60	19.37 ± 0.93
D 11	Total nitrogen (µg/l)	1191.43 ± 198.43	1068.00 ± 41.40
	Total phosphorus (µg/l)	183.07 ± 50.81	43.40 ± 1.89
	Calcium (mg/l)	11.86 ± 1.12	20.46 ± 1.88
	Sodium (mg/l)	0.83 ± 0.11	0.78 ± 0.25
	Magnesium (mg/l)	3.98 ± 0.25	8.04 ± 0.69
	Potassium (mg/l)	1.39 ± 0.26	1.58 ± 0.35
	Chloride (mg/l)	2.04 ± 0.35	1.72 ± 0.19
	Sulfate (mg/l)	4.14 ± 0.45	33.36 ± 9.10
	Chlorophyll (µg/l)	4.84 ± 1.08	4.44 ± 1.68
	Non-volatile suspended solids (mg/l)	1.18 ± 0.41	0.44 ± 0.20
	Volatile suspended solids (mg/l)	1.19 ± 0.17	1.08 ± 0.33
	Total suspended solids (mg/l)	2.37 ± 0.53	1.52 ± 0.51
	Conductivity (µS/mol)	97.07 ± 6.12	148.24 ± 18.31
	pH	7.67 ± 0.27	7.66 ± 0.25
	Temperature (° C)	16.73 ± 1.28	21.60 ± 1.78
D 12	Total nitrogen (µg/l)	1040.00 ± 280.62	1120.00 ± 110.48
	Total phosphorus (µg/l)	154.67 ± 90.73	61.50 ± 16.47
	Calcium (mg/l)	8.60 ± 2.17	25.00 ± 7.53
	Sodium (mg/l)	1.26 ± 0.42	0.98 ± 0.29
	Magnesium (mg/l)	3.22 ± 0.63	7.67 ± 2.11
	Potassium (mg/l)	2.54 ± 0.73	2.37 ± 1.01

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 12	Chloride (mg/l)	1.29 ± 0.19	0.82 ± 0.15
	Sulfate (mg/l)	4.64 ± 1.12	82.38 ± 26.76
	Chlorophyll (µg/l)	13.99 ± 4.28	11.48 ± 5.36
	Non-volatile suspended solids (mg/l)	23.03 ± 19.90	1.07 ± 0.31
	Volatile suspended solids (mg/l)	7.84 ± 4.25	4.22 ± 1.64
	Total suspended solids (mg/l)	30.87 ± 24.05	5.28 ± 1.61
	Conductivity (µS/mol)	77.20 ± 13.05	197.22 ± 55.71
	pH	6.61 ± 0.16	6.52 ± 0.53
	Temperature (° C)	16.30 ± 1.52	20.68 ± 1.55
D 13	Total nitrogen (µg/l)	754.44 ± 142.03	1273.33 ± 99.96
	Total phosphorus (µg/l)	57.60 ± 5.42	71.50 ± 5.82
	Calcium (mg/l)	14.03 ± 2.31	19.37 ± 1.94
	Sodium (mg/l)	1.03 ± 0.12	1.02 ± 0.26
	Magnesium (mg/l)	5.73 ± 1.14	7.05 ± 0.66
	Potassium (mg/l)	1.82 ± 0.42	2.32 ± 0.49
	Chloride (mg/l)	1.01 ± 0.14	1.84 ± 0.20
	Sulfate (mg/l)	3.96 ± 0.86	9.27 ± 4.61
	Chlorophyll (µg/l)	3.85 ± 0.67	5.02 ± 0.82
	Non-volatile suspended solids (mg/l)	2.75 ± 1.55	0.85 ± 0.13
	Volatile suspended solids (mg/l)	1.49 ± 0.53	1.68 ± 0.40
	Total suspended solids (mg/l)	4.24 ± 1.98	2.53 ± 0.49
	Conductivity (µS/mol)	96.90 ± 9.93	139.32 ± 13.67
	pH	7.48 ± 0.41	7.57 ± 0.17
	Temperature (° C)	15.40 ± 1.38	20.97 ± 1.04
D 14	Total nitrogen (µg/l)	985.00 ± 219.31	1604.00 ± 191.07
	Total phosphorus (µg/l)	76.83 ± 18.06	55.60 ± 5.89
	Calcium (mg/l)	13.09 ± 3.52	17.44 ± 4.20
	Sodium (mg/l)	1.22 ± 0.28	1.12 ± 0.43

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 14	Magnesium (mg/l)	4.30 ± 0.93	6.50 ± 1.43
	Potassium (mg/l)	3.19 ± 0.56	3.88 ± 0.84
	Chloride (mg/l)	1.17 ± 0.23	2.08 ± 0.38
	Sulfate (mg/l)	3.64 ± 1.06	42.70 ± 12.52
	Chlorophyll (µg/l)	5.87 ± 1.49	4.96 ± 1.32
	Non-volatile suspended solids (mg/l)	1.86 ± 0.76	0.75 ± 0.28
	Volatile suspended solids (mg/l)	1.50 ± 0.44	1.23 ± 0.17
	Total suspended solids (mg/l)	3.36 ± 1.13	1.98 ± 0.43
	Conductivity (µS/mol)	104.43 ± 21.62	138.40 ± 32.44
	pH	7.37 ± 0.18	7.87 ± 0.58
	Temperature (° C)	15.86 ± 1.01	22.36 ± 1.19
D 15	Total nitrogen (µg/l)	1007.14 ± 333.45	1106.88 ± 30.68
	Total phosphorus (µg/l)	73.20 ± 6.98	63.50 ± 3.16
	Calcium (mg/l)	18.02 ± 2.02	20.78 ± 0.83
	Sodium (mg/l)	0.96 ± 0.15	1.53 ± 0.34
	Magnesium (mg/l)	6.32 ± 0.89	7.91 ± 0.34
	Potassium (mg/l)	1.48 ± 0.41	1.38 ± 0.13
	Chloride (mg/l)	1.40 ± 0.31	1.67 ± 0.09
	Sulfate (mg/l)	4.35 ± 1.36	23.98 ± 5.64
	Chlorophyll (µg/l)	7.77 ± 2.75	5.83 ± 1.33
	Non-volatile suspended solids (mg/l)	1.49 ± 0.58	0.54 ± 0.06
	Volatile suspended solids (mg/l)	2.07 ± 0.47	1.62 ± 0.23
	Total suspended solids (mg/l)	3.56 ± 0.84	2.16 ± 0.27
	Conductivity (µS/mol)	124.40 ± 8.32	150.69 ± 8.88
	pH	7.34 ± 0.27	8.03 ± 0.21
	Temperature (° C)	15.90 ± 1.35	20.56 ± 0.76
D 18	Total nitrogen (µg/l)	980.00 ± 293.18	2408.33 ± 960.21
	Total phosphorus (µg/l)	50.20 ± 6.29	149.83 ± 80.84

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 18	Calcium (mg/l)	10.97 ± 3.80	14.75 ± 3.12
	Sodium (mg/l)	1.27 ± 0.23	1.17 ± 0.35
	Magnesium (mg/l)	3.65 ± 1.07	5.25 ± 1.12
	Potassium (mg/l)	1.60 ± 0.20	2.66 ± 0.64
	Chloride (mg/l)	1.19 ± 0.19	1.36 ± 0.16
	Sulfate (mg/l)	3.68 ± 0.89	29.98 ± 11.99
	Chlorophyll (µg/l)	6.48 ± 1.27	150.05 ± 124.27
	Non-volatile suspended solids (mg/l)	2.11 ± 0.57	2.65 ± 1.56
	Volatile suspended solids (mg/l)	1.51 ± 0.28	11.98 ± 9.83
	Total suspended solids (mg/l)	3.62 ± 0.71	14.63 ± 11.34
	Conductivity (µS/mol)	64.60 ± 11.56	127.77 ± 26.10
	pH	7.12 ± 0.17	8.10 ± 0.38
	Temperature (° C)	14.80 ± 1.04	20.38 ± 1.29
D 19	Total nitrogen (µg/l)	1132.00 ± 587.99	4680.00 ± 2080.00
	Total phosphorus (µg/l)	42.67 ± 6.61	1084.50 ± 331.50
	Calcium (mg/l)	12.06 ± 1.64	11.20 ± 1.00
	Sodium (mg/l)	1.40 ± 0.15	5.50 ± 1.10
	Magnesium (mg/l)	4.46 ± 0.53	3.95 ± 0.45
	Potassium (mg/l)	1.53 ± 0.67	2.15 ± 0.75
	Chloride (mg/l)	1.33 ± 0.25	4.01 ± 0.31
	Sulfate (mg/l)	2.57 ± 1.10	0.00 ± 0.00
	Chlorophyll (µg/l)	6.80 ± 1.31	609.40 ± 100.40
	Non-volatile suspended solids (mg/l)	2.66 ± 0.74	35.15 ± 0.15
	Volatile suspended solids (mg/l)	2.87 ± 0.62	87.70 ± 11.00
	Total suspended solids (mg/l)	5.53 ± 1.17	122.85 ± 10.85
	Conductivity (µS/mol)	96.86 ± 11.18	60.00 ± 8.00
	pH	6.57 ± 0.07	7.43 ± 0.07
	Temperature (° C)	14.86 ± 0.91	27.55 ± 0.35

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 23	Total nitrogen (µg/l)	765.00 ± 277.29	1878.00 ± 230.18
	Total phosphorus (µg/l)	63.50 ± 12.57	64.40 ± 12.73
	Calcium (mg/l)	10.00 ± 1.42	15.22 ± 2.61
	Sodium (mg/l)	1.08 ± 0.29	2.86 ± 0.31
	Magnesium (mg/l)	3.27 ± 0.54	5.36 ± 0.76
	Potassium (mg/l)	1.95 ± 0.53	0.76 ± 0.49
	Chloride (mg/l)	1.30 ± 0.23	2.58 ± 0.37
	Sulfate (mg/l)	3.33 ± 1.16	0.00 ± 0.00
	Chlorophyll (µg/l)	6.79 ± 1.78	14.10 ± 6.31
	Non-volatile suspended solids (mg/l)	5.29 ± 2.63	2.36 ± 0.99
	Volatile suspended solids (mg/l)	3.36 ± 1.23	5.50 ± 1.41
	Total suspended solids (mg/l)	8.64 ± 3.77	7.86 ± 2.34
	Conductivity (µS/mol)	79.71 ± 7.87	98.42 ± 16.15
	pH	6.33 ± 0.09	6.60 ± 0.12
	Temperature (° C)	16.43 ± 1.04	18.40 ± 0.85
D 24	Total nitrogen (µg/l)	505.71 ± 71.18	2386.67 ± 196.41
	Total phosphorus (µg/l)	62.67 ± 5.54	47.33 ± 2.91
	Calcium (mg/l)	8.75 ± 1.78	13.90 ± 0.21
	Sodium (mg/l)	1.22 ± 0.23	1.80 ± 0.17
	Magnesium (mg/l)	2.98 ± 0.41	4.73 ± 0.07
	Potassium (mg/l)	1.46 ± 0.48	1.13 ± 0.17
	Chloride (mg/l)	1.46 ± 0.16	3.35 ± 0.27
	Sulfate (mg/l)	3.18 ± 0.84	0.00 ± 0.00
	Chlorophyll (µg/l)	7.36 ± 1.94	8.43 ± 3.58
	Non-volatile suspended solids (mg/l)	3.20 ± 1.03	1.67 ± 0.67
	Volatile suspended solids (mg/l)	2.29 ± 0.69	3.03 ± 0.24
	Total suspended solids (mg/l)	5.49 ± 1.52	4.70 ± 0.74
	Conductivity (µS/mol)	67.14 ± 11.19	83.77 ± 0.61

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 24	pH	6.11 ± 0.08	6.32 ± 0.13
	Temperature (° C)	14.00 ± 1.33	22.27 ± 1.14
D 26	Total nitrogen (µg/l)	1163.85 ± 110.53	1488.00 ± 88.06
	Total phosphorus (µg/l)	336.71 ± 92.24	250.80 ± 64.05
	Calcium (mg/l)	20.85 ± 1.34	27.50 ± 1.95
	Sodium (mg/l)	0.82 ± 0.13	1.22 ± 0.38
	Magnesium (mg/l)	7.53 ± 0.85	10.16 ± 0.84
	Potassium (mg/l)	1.33 ± 0.31	3.38 ± 0.84
	Chloride (mg/l)	2.06 ± 0.30	1.93 ± 0.21
	Sulfate (mg/l)	3.56 ± 0.56	15.60 ± 12.60
	Chlorophyll (µg/l)	6.63 ± 1.75	6.36 ± 1.82
	Non-volatile suspended solids (mg/l)	2.86 ± 1.34	0.74 ± 0.17
	Volatile suspended solids (mg/l)	1.70 ± 0.27	2.18 ± 0.53
	Total suspended solids (mg/l)	4.56 ± 1.55	2.92 ± 0.61
	Conductivity (µS/mol)	148.53 ± 5.69	192.80 ± 20.45
	pH	7.87 ± 0.24	7.18 ± 0.07
	Temperature (° C)	16.40 ± 1.23	19.98 ± 0.98
D 27	Total nitrogen (µg/l)	800.00 ± 162.17	1235.00 ± 102.33
	Total phosphorus (µg/l)	99.38 ± 18.15	53.83 ± 4.32
	Calcium (mg/l)	17.71 ± 2.18	14.83 ± 1.07
	Sodium (mg/l)	1.18 ± 0.15	0.95 ± 0.19
	Magnesium (mg/l)	5.98 ± 1.22	5.52 ± 0.36
	Potassium (mg/l)	1.76 ± 0.47	2.43 ± 0.32
	Chloride (mg/l)	1.27 ± 0.18	1.54 ± 0.11
	Sulfate (mg/l)	3.50 ± 0.35	15.88 ± 3.29
	Chlorophyll (µg/l)	4.71 ± 0.86	11.07 ± 3.22
	Non-volatile suspended solids (mg/l)	3.50 ± 1.78	0.53 ± 0.16
	Volatile suspended solids (mg/l)	2.01 ± 0.29	3.00 ± 0.92

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 27	Total suspended solids (mg/l)	5.51 ± 2.00	3.53 ± 1.03
	Conductivity (µS/mol)	112.60 ± 4.35	112.87 ± 7.87
	pH	8.03 ± 0.40	7.82 ± 0.21
	Temperature (° C)	15.90 ± 1.08	19.43 ± 0.73
D 34	Total nitrogen (µg/l)	1242.86 ± 456.12	1793.33 ± 72.51
	Total phosphorus (µg/l)	35.33 ± 5.21	48.17 ± 9.22
	Calcium (mg/l)	23.36 ± 1.92	30.12 ± 2.00
	Sodium (mg/l)	2.51 ± 0.22	4.05 ± 0.25
	Magnesium (mg/l)	8.49 ± 1.04	10.82 ± 0.68
	Potassium (mg/l)	0.71 ± 0.21	3.68 ± 0.14
	Chloride (mg/l)	1.53 ± 0.26	2.67 ± 0.08
	Sulfate (mg/l)	2.34 ± 0.29	0.00 ± 0.00
	Chlorophyll (µg/l)	3.93 ± 1.18	3.60 ± 0.66
	Non-volatile suspended solids (mg/l)	1.83 ± 0.62	0.73 ± 0.16
	Volatile suspended solids (mg/l)	2.23 ± 0.88	1.93 ± 0.38
	Total suspended solids (mg/l)	4.06 ± 1.45	2.67 ± 0.50
	Conductivity (µS/mol)	169.71 ± 18.67	203.53 ± 12.20
	pH	7.13 ± 0.11	7.19 ± 0.17
	Temperature (° C)	14.57 ± 0.90	21.85 ± 0.84
D 35	Total nitrogen (µg/l)	1474.62 ± 196.02	1616.25 ± 78.65
	Total phosphorus (µg/l)	237.46 ± 53.73	74.38 ± 4.79
	Calcium (mg/l)	16.97 ± 1.11	15.74 ± 0.69
	Sodium (mg/l)	2.39 ± 0.13	1.60 ± 0.13
	Magnesium (mg/l)	6.62 ± 0.41	5.78 ± 0.29
	Potassium (mg/l)	3.25 ± 0.22	1.92 ± 0.21
	Chloride (mg/l)	1.97 ± 0.29	1.37 ± 0.07
	Sulfate (mg/l)	2.29 ± 0.32	4.18 ± 1.34
	Chlorophyll (µg/l)	10.71 ± 1.61	17.16 ± 5.41

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
D 35	Non-volatile suspended solids (mg/l)	2.08 ± 0.79	0.86 ± 0.23
	Volatile suspended solids (mg/l)	2.25 ± 0.58	4.08 ± 0.87
	Total suspended solids (mg/l)	4.33 ± 1.12	4.94 ± 1.03
	Conductivity (µS/mol)	140.13 ± 4.32	122.41 ± 5.38
	pH	8.75 ± 0.26	9.39 ± 0.26
	Temperature (° C)	16.07 ± 1.17	19.71 ± 0.71
D 38	Total nitrogen (µg/l)	896.67 ± 332.88	660.00 ± 19.24
	Total phosphorus (µg/l)	28.50 ± 6.50	15.40 ± 2.32
	Calcium (mg/l)	10.50 ± 1.42	24.26 ± 1.43
	Sodium (mg/l)	3.30 ± 0.55	6.20 ± 0.59
	Magnesium (mg/l)	6.13 ± 1.23	11.94 ± 0.86
	Potassium (mg/l)	4.43 ± 0.57	7.44 ± 0.29
	Chloride (mg/l)	1.70 ± 0.85	2.37 ± 0.11
	Sulfate (mg/l)	0.40 ± 0.00	0.00 ± 0.00
	Chlorophyll (µg/l)	1.20 ± 0.26	1.52 ± 0.37
	Non-volatile suspended solids (mg/l)	1.17 ± 1.02	0.24 ± 0.08
	Volatile suspended solids (mg/l)	0.07 ± 0.07	1.00 ± 0.14
	Total suspended solids (mg/l)	1.23 ± 1.09	1.24 ± 0.21
	Conductivity (µS/mol)	138.33 ± 15.90	237.22 ± 14.63
	pH	7.20 ± 0.21	7.95 ± 0.13
	Temperature (° C)	13.67 ± 1.86	18.92 ± 0.85
F 1	Total nitrogen (µg/l)	1030.00 ± 164.78	2633.33 ± 213.75
	Total phosphorus (µg/l)	18.25 ± 6.03	29.90 ± 1.90
	Calcium (mg/l)	46.16 ± 4.27	53.34 ± 2.66
	Sodium (mg/l)	6.34 ± 0.96	12.88 ± 1.01
	Magnesium (mg/l)	13.41 ± 1.53	28.21 ± 1.91
	Potassium (mg/l)	2.22 ± 0.20	4.18 ± 0.34
	Chloride (mg/l)	4.40 ± 0.76	11.46 ± 0.97

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
F 1	Sulfate (mg/l)	2.01 ± 0.15	0.02 ± 0.02
	Chlorophyll (µg/l)	1.71 ± 0.29	6.99 ± 1.48
	Non-volatile suspended solids (mg/l)	0.34 ± 0.09	1.00 ± 0.32
	Volatile suspended solids (mg/l)	0.66 ± 0.09	2.97 ± 0.46
	Total suspended solids (mg/l)	1.00 ± 0.11	3.97 ± 0.74
	Conductivity (µS/mol)	310.70 ± 7.92	428.70 ± 16.76
	pH	8.15 ± 0.08	8.59 ± 0.15
	Temperature (° C)	16.50 ± 1.12	19.73 ± 0.68
F 2	Total nitrogen (µg/l)	852.86 ± 126.20	1511.67 ± 41.10
	Total phosphorus (µg/l)	21.57 ± 9.30	20.00 ± 1.32
	Calcium (mg/l)	54.43 ± 3.01	44.13 ± 8.25
	Sodium (mg/l)	2.70 ± 0.12	6.27 ± 0.27
	Magnesium (mg/l)	8.51 ± 0.40	13.60 ± 0.41
	Potassium (mg/l)	1.03 ± 0.09	1.90 ± 0.13
	Chloride (mg/l)	1.82 ± 0.33	5.83 ± 0.50
	Sulfate (mg/l)	2.36 ± 0.26	454.83 ± 454.83
	Chlorophyll (µg/l)	1.69 ± 0.29	5.62 ± 1.72
	Non-volatile suspended solids (mg/l)	0.29 ± 0.13	0.30 ± 0.14
	Volatile suspended solids (mg/l)	0.54 ± 0.09	1.90 ± 0.34
	Total suspended solids (mg/l)	0.83 ± 0.21	2.20 ± 0.46
	Conductivity (µS/mol)	272.50 ± 14.28	294.67 ± 38.70
	pH	8.13 ± 0.08	9.02 ± 0.31
	Temperature (° C)	18.13 ± 1.29	20.37 ± 1.19
F 3	Total nitrogen (µg/l)	2007.14 ± 283.92	2386.67 ± 121.78
	Total phosphorus (µg/l)	71.57 ± 25.05	22.33 ± 0.80
	Calcium (mg/l)	49.63 ± 4.42	56.33 ± 0.91
	Sodium (mg/l)	13.79 ± 1.18	17.07 ± 1.32
	Magnesium (mg/l)	27.13 ± 2.06	38.85 ± 1.39

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
F 3	Potassium (mg/l)	8.60 ± 0.70	8.73 ± 0.43
	Chloride (mg/l)	6.90 ± 1.34	12.21 ± 0.78
	Sulfate (mg/l)	2.63 ± 0.23	0.17 ± 0.17
	Chlorophyll (µg/l)	21.79 ± 11.39	1.42 ± 0.20
	Non-volatile suspended solids (mg/l)	1.19 ± 0.39	0.10 ± 0.05
	Volatile suspended solids (mg/l)	7.83 ± 4.90	0.73 ± 0.07
	Total suspended solids (mg/l)	9.01 ± 5.25	0.83 ± 0.11
	Conductivity (µS/mol)	445.56 ± 17.69	532.33 ± 17.60
	pH	8.33 ± 0.12	8.66 ± 0.12
	Temperature (° C)	17.78 ± 1.10	19.47 ± 1.08
F 4	Total nitrogen (µg/l)	2271.43 ± 292.19	2360.00 ± 126.60
	Total phosphorus (µg/l)	80.71 ± 10.70	18.17 ± 0.54
	Calcium (mg/l)	53.93 ± 4.81	30.53 ± 1.33
	Sodium (mg/l)	19.69 ± 2.40	18.68 ± 0.95
	Magnesium (mg/l)	37.24 ± 2.32	43.18 ± 1.97
	Potassium (mg/l)	12.94 ± 1.66	12.73 ± 0.60
	Chloride (mg/l)	10.50 ± 1.05	13.95 ± 0.67
	Sulfate (mg/l)	3.22 ± 0.56	0.00 ± 0.00
	Chlorophyll (µg/l)	18.64 ± 2.96	1.73 ± 0.23
	Non-volatile suspended solids (mg/l)	1.47 ± 0.55	0.07 ± 0.03
	Volatile suspended solids (mg/l)	9.17 ± 2.72	0.83 ± 0.11
	Total suspended solids (mg/l)	10.64 ± 2.70	0.90 ± 0.14
	Conductivity (µS/mol)	532.00 ± 25.02	476.17 ± 13.15
	pH	8.33 ± 0.08	8.99 ± 0.15
	Temperature (° C)	17.78 ± 1.10	19.67 ± 1.07
F 6	Total nitrogen (µg/l)	1488.57 ± 235.32	2253.64 ± 106.03
	Total phosphorus (µg/l)	64.86 ± 9.73	42.45 ± 3.46
	Calcium (mg/l)	49.96 ± 4.05	34.58 ± 4.94

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
F 6	Sodium (mg/l)	4.17 ± 0.72	10.99 ± 0.46
	Magnesium (mg/l)	9.06 ± 0.66	18.05 ± 0.50
	Potassium (mg/l)	2.45 ± 0.19	3.99 ± 0.17
	Chloride (mg/l)	2.10 ± 0.29	6.71 ± 0.27
	Sulfate (mg/l)	2.32 ± 0.32	0.00 ± 0.00
	Chlorophyll (µg/l)	15.69 ± 2.40	12.67 ± 2.63
	Non-volatile suspended solids (mg/l)	1.90 ± 0.85	0.88 ± 0.15
	Volatile suspended solids (mg/l)	10.63 ± 2.91	6.63 ± 1.66
	Total suspended solids (mg/l)	12.53 ± 2.83	7.51 ± 1.72
	Conductivity (µS/mol)	272.11 ± 6.19	294.82 ± 23.64
	pH	8.22 ± 0.12	9.34 ± 0.20
	Temperature (° C)	16.56 ± 1.44	18.65 ± 0.54
F 7	Total nitrogen (µg/l)	2010.00 ± 180.83	2088.33 ± 160.07
	Total phosphorus (µg/l)	110.67 ± 16.56	27.67 ± 2.23
	Calcium (mg/l)	67.80 ± 0.84	98.60 ± 17.49
	Sodium (mg/l)	3.22 ± 0.08	25.45 ± 6.13
	Magnesium (mg/l)	8.63 ± 1.21	50.30 ± 7.61
	Potassium (mg/l)	2.44 ± 0.12	12.47 ± 0.77
	Chloride (mg/l)	NA	19.03 ± 2.02
	Sulfate (mg/l)	NA	190.03 ± 38.77
	Chlorophyll (µg/l)	22.93 ± 4.85	2.63 ± 0.34
	Non-volatile suspended solids (mg/l)	2.53 ± 1.79	0.10 ± 0.04
	Volatile suspended solids (mg/l)	14.23 ± 2.99	0.77 ± 0.03
	Total suspended solids (mg/l)	16.77 ± 2.61	0.87 ± 0.06
	Conductivity (µS/mol)	273.00 ± 7.68	849.50 ± 62.13
	pH	8.30 ± 0.12	8.30 ± 0.08
	Temperature (° C)	17.20 ± 1.16	20.25 ± 1.33
F 10	Total nitrogen (µg/l)	1712.86 ± 220.22	2246.67 ± 331.79

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
F 10	Total phosphorus (µg/l)	42.57 ± 9.80	31.00 ± 2.18
	Calcium (mg/l)	20.19 ± 2.28	34.95 ± 12.22
	Sodium (mg/l)	42.06 ± 4.04	48.60 ± 10.28
	Magnesium (mg/l)	55.17 ± 5.28	80.67 ± 14.15
	Potassium (mg/l)	12.57 ± 0.82	12.95 ± 1.57
	Chloride (mg/l)	13.40 ± 2.21	25.24 ± 4.52
	Sulfate (mg/l)	2.56 ± 0.29	33.97 ± 33.97
	Chlorophyll (µg/l)	2.84 ± 0.95	1.80 ± 0.23
	Non-volatile suspended solids (mg/l)	1.01 ± 0.47	0.20 ± 0.04
	Volatile suspended solids (mg/l)	2.74 ± 1.01	0.95 ± 0.15
	Total suspended solids (mg/l)	3.76 ± 1.42	1.15 ± 0.16
	Conductivity (µS/mol)	688.00 ± 39.18	818.40 ± 125.88
	pH	9.16 ± 0.11	9.34 ± 0.10
	Temperature (° C)	16.00 ± 1.25	19.62 ± 0.82
F 11	Total nitrogen (µg/l)	2587.50 ± 504.78	3131.67 ± 353.26
	Total phosphorus (µg/l)	101.67 ± 55.86	43.67 ± 4.92
	Calcium (mg/l)	24.10 ± 0.72	33.10 ± 2.26
	Sodium (mg/l)	33.64 ± 4.12	35.37 ± 4.99
	Magnesium (mg/l)	47.73 ± 6.93	62.60 ± 9.19
	Potassium (mg/l)	16.00 ± 1.66	19.07 ± 2.04
	Chloride (mg/l)	NA	18.45 ± 2.42
	Sulfate (mg/l)	NA	0.00 ± 0.00
	Chlorophyll (µg/l)	3.18 ± 1.03	2.37 ± 0.41
	Non-volatile suspended solids (mg/l)	1.10 ± 0.21	0.42 ± 0.23
	Volatile suspended solids (mg/l)	1.97 ± 1.02	1.60 ± 0.59
	Total suspended solids (mg/l)	3.07 ± 1.08	2.02 ± 0.81
	Conductivity (µS/mol)	508.00 ± 64.37	587.33 ± 103.04
	pH	9.80 ± 0.12	8.98 ± 0.21

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
F 11	Temperature (° C)	16.40 ± 2.16	18.48 ± 0.86
F 12	Total nitrogen (µg/l)	1584.00 ± 515.79	4376.67 ± 661.00
	Total phosphorus (µg/l)	99.00 ± 29.57	56.00 ± 3.40
	Calcium (mg/l)	205.81 ± 186.45	253.92 ± 32.76
	Sodium (mg/l)	61.37 ± 14.57	16.85 ± 2.61
	Magnesium (mg/l)	86.35 ± 18.48	71.42 ± 10.86
	Potassium (mg/l)	34.45 ± 4.46	20.22 ± 3.37
	Chloride (mg/l)	16.00 ± 5.02	19.31 ± 2.96
	Sulfate (mg/l)	27.26 ± 18.21	528.97 ± 84.78
	Chlorophyll (µg/l)	4.58 ± 1.29	2.70 ± 1.20
	Non-volatile suspended solids (mg/l)	1.48 ± 0.62	0.90 ± 0.23
	Volatile suspended solids (mg/l)	4.40 ± 0.97	2.32 ± 0.29
	Total suspended solids (mg/l)	5.88 ± 1.57	3.22 ± 0.50
	Conductivity (µS/mol)	1140.20 ± 282.60	1435.67 ± 168.04
	pH	9.20 ± 0.34	9.04 ± 0.32
	Temperature (° C)	15.60 ± 2.50	20.02 ± 1.22
H 3	Total nitrogen (µg/l)	3167.50 ± 1332.57	23585.00 ± 10660.80
	Total phosphorus (µg/l)	2534.38 ± 542.18	8059.00 ± 3255.42
	Calcium (mg/l)	9.14 ± 2.85	0.78 ± 0.32
	Sodium (mg/l)	2828.26 ± 526.04	8127.83 ± 4192.32
	Magnesium (mg/l)	26.82 ± 4.68	16.15 ± 4.93
	Potassium (mg/l)	117.53 ± 21.10	222.23 ± 108.24
	Chloride (mg/l)	2.88 ± 0.43	1072.53 ± 511.44
	Sulfate (mg/l)	24.93 ± 2.48	10.65 ± 6.31
	Chlorophyll (µg/l)	10.33 ± 2.37	29.55 ± 4.41
	Non-volatile suspended solids (mg/l)	82.14 ± 32.39	131.53 ± 64.14
	Volatile suspended solids (mg/l)	31.20 ± 13.67	71.08 ± 26.17
	Total suspended solids (mg/l)	113.34 ± 42.56	202.60 ± 90.00

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
H 3	Conductivity (µS/mol)	8224.56 ± 684.75	3300.00 ± 856.36
	pH	10.00 ± 0.00	9.93 ± 0.11
	Temperature (° C)	15.78 ± 1.91	22.70 ± 1.91
H 4	Total nitrogen (µg/l)	1832.22 ± 216.36	5074.00 ± 706.06
	Total phosphorus (µg/l)	328.78 ± 90.09	1368.80 ± 297.13
	Calcium (mg/l)	6.36 ± 0.72	7.02 ± 0.92
	Sodium (mg/l)	121.85 ± 11.31	170.52 ± 19.37
	Magnesium (mg/l)	35.32 ± 3.18	57.30 ± 4.80
	Potassium (mg/l)	11.51 ± 0.85	14.00 ± 0.78
	Chloride (mg/l)	12.90 ± 3.03	33.44 ± 4.30
	Sulfate (mg/l)	6.00 ± 1.28	0.00 ± 0.00
	Chlorophyll (µg/l)	9.11 ± 5.41	8.32 ± 2.97
	Non-volatile suspended solids (mg/l)	0.43 ± 0.20	2.18 ± 1.62
	Volatile suspended solids (mg/l)	1.06 ± 0.38	3.36 ± 1.64
	Total suspended solids (mg/l)	1.49 ± 0.57	5.54 ± 3.25
	Conductivity (µS/mol)	746.50 ± 58.18	909.60 ± 64.97
	pH	8.17 ± 0.11	8.25 ± 0.14
	Temperature (° C)	15.90 ± 1.39	19.96 ± 1.09
H 6	Total nitrogen (µg/l)	1478.89 ± 207.28	2542.00 ± 333.46
	Total phosphorus (µg/l)	124.44 ± 15.82	629.00 ± 250.93
	Calcium (mg/l)	15.02 ± 1.18	33.64 ± 11.71
	Sodium (mg/l)	9.61 ± 1.34	14.70 ± 3.13
	Magnesium (mg/l)	12.66 ± 1.38	51.06 ± 15.32
	Potassium (mg/l)	10.15 ± 0.97	14.70 ± 2.15
	Chloride (mg/l)	2.20 ± 0.25	4.73 ± 0.85
	Sulfate (mg/l)	3.42 ± 0.43	82.20 ± 34.10
	Chlorophyll (µg/l)	9.44 ± 3.18	14.18 ± 4.83
	Non-volatile suspended solids (mg/l)	3.16 ± 1.66	0.86 ± 0.65

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
H 6	Volatile suspended solids (mg/l)	3.30 ± 1.18	2.20 ± 0.69
	Total suspended solids (mg/l)	6.46 ± 2.51	3.06 ± 1.06
	Conductivity (µS/mol)	204.30 ± 15.88	509.80 ± 183.13
	pH	8.80 ± 0.34	8.41 ± 0.29
	Temperature (° C)	16.00 ± 1.57	19.64 ± 1.09
H 11	Total nitrogen (µg/l)	2512.22 ± 255.97	3641.67 ± 194.82
	Total phosphorus (µg/l)	199.11 ± 51.91	150.00 ± 40.27
	Calcium (mg/l)	10.50 ± 2.00	11.17 ± 0.94
	Sodium (mg/l)	197.45 ± 17.73	188.22 ± 10.15
	Magnesium (mg/l)	88.47 ± 7.90	98.71 ± 4.86
	Potassium (mg/l)	11.68 ± 1.58	6.01 ± 0.40
	Chloride (mg/l)	15.20 ± 4.53	31.87 ± 1.55
	Sulfate (mg/l)	51.31 ± 12.71	5.17 ± 2.98
	Chlorophyll (µg/l)	12.28 ± 6.68	18.48 ± 6.47
	Non-volatile suspended solids (mg/l)	1.30 ± 0.52	1.23 ± 0.24
	Volatile suspended solids (mg/l)	4.88 ± 1.89	5.64 ± 1.43
	Total suspended solids (mg/l)	6.18 ± 2.38	6.88 ± 1.64
	Conductivity (µS/mol)	1170.10 ± 144.63	1147.83 ± 58.73
	pH	9.55 ± 0.14	9.55 ± 0.12
	Temperature (° C)	15.20 ± 1.20	20.12 ± 0.88
H 13	Total nitrogen (µg/l)	3208.75 ± 196.27	8628.33 ± 883.51
	Total phosphorus (µg/l)	820.00 ± 143.04	1840.58 ± 450.57
	Calcium (mg/l)	9.19 ± 1.35	7.43 ± 0.77
	Sodium (mg/l)	297.29 ± 24.69	303.93 ± 30.88
	Magnesium (mg/l)	90.09 ± 9.92	81.06 ± 5.05
	Potassium (mg/l)	27.13 ± 2.61	31.42 ± 2.13
	Chloride (mg/l)	12.20 ± 7.27	51.74 ± 5.29
	Sulfate (mg/l)	43.56 ± 8.79	85.06 ± 16.04

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
H 13	Chlorophyll (µg/l)	7.18 ± 2.32	9.49 ± 2.19
	Non-volatile suspended solids (mg/l)	3.12 ± 0.85	2.35 ± 0.61
	Volatile suspended solids (mg/l)	6.83 ± 1.48	5.45 ± 0.90
	Total suspended solids (mg/l)	9.96 ± 2.02	7.80 ± 1.38
	Conductivity (µS/mol)	1658.60 ± 110.84	1414.83 ± 127.75
	pH	9.48 ± 0.11	8.93 ± 0.19
	Temperature (° C)	17.40 ± 1.07	19.31 ± 0.84
H 14	Total nitrogen (µg/l)	2713.33 ± 677.40	6332.50 ± 784.00
	Total phosphorus (µg/l)	1291.11 ± 263.79	320.38 ± 105.19
	Calcium (mg/l)	8.98 ± 1.27	16.55 ± 1.80
	Sodium (mg/l)	563.00 ± 42.36	358.99 ± 39.24
	Magnesium (mg/l)	148.14 ± 13.04	204.35 ± 23.95
	Potassium (mg/l)	18.94 ± 1.52	9.84 ± 1.35
	Chloride (mg/l)	12.00 ± 4.78	77.55 ± 6.97
	Sulfate (mg/l)	79.56 ± 15.98	396.29 ± 49.55
	Chlorophyll (µg/l)	21.01 ± 5.68	5.93 ± 1.26
	Non-volatile suspended solids (mg/l)	5.21 ± 0.93	2.45 ± 1.61
	Volatile suspended solids (mg/l)	17.48 ± 4.01	5.53 ± 2.41
	Total suspended solids (mg/l)	22.69 ± 4.58	7.98 ± 3.95
	Conductivity (µS/mol)	3050.00 ± 207.09	2042.38 ± 178.69
	pH	9.55 ± 0.08	9.26 ± 0.19
	Temperature (° C)	14.67 ± 1.55	20.61 ± 1.23
H 16	Total nitrogen (µg/l)	1444.44 ± 166.48	2401.25 ± 157.89
	Total phosphorus (µg/l)	463.56 ± 344.36	93.50 ± 11.76
	Calcium (mg/l)	17.17 ± 3.70	14.18 ± 1.36
	Sodium (mg/l)	87.34 ± 10.65	102.34 ± 5.45
	Magnesium (mg/l)	40.24 ± 2.02	66.58 ± 3.53
	Potassium (mg/l)	3.95 ± 0.26	3.31 ± 0.30

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
H 16	Chloride (mg/l)	8.23 ± 0.93	12.20 ± 0.94
	Sulfate (mg/l)	6.53 ± 1.36	0.00 ± 0.00
	Chlorophyll (µg/l)	24.48 ± 7.28	19.74 ± 6.99
	Non-volatile suspended solids (mg/l)	2.12 ± 1.14	1.41 ± 0.54
	Volatile suspended solids (mg/l)	6.76 ± 2.50	4.95 ± 1.13
	Total suspended solids (mg/l)	8.88 ± 3.48	6.36 ± 1.57
	Conductivity (µS/mol)	656.18 ± 42.01	760.50 ± 41.53
	pH	9.62 ± 0.15	9.49 ± 0.18
	Temperature (° C)	15.90 ± 1.48	19.76 ± 0.71
L 5	Total nitrogen (µg/l)	292.00 ± 35.41	816.00 ± 59.88
	Total phosphorus (µg/l)	30.50 ± 9.44	24.80 ± 2.06
	Calcium (mg/l)	6.99 ± 0.68	9.42 ± 0.41
	Sodium (mg/l)	1.21 ± 0.07	1.48 ± 0.28
	Magnesium (mg/l)	2.67 ± 0.23	4.00 ± 0.19
	Potassium (mg/l)	3.19 ± 0.19	7.96 ± 0.77
	Chloride (mg/l)	0.63 ± 0.10	1.37 ± 0.20
	Sulfate (mg/l)	0.44 ± 0.10	0.00 ± 0.00
	Chlorophyll (µg/l)	5.54 ± 1.92	1.68 ± 0.17
	Non-volatile suspended solids (mg/l)	0.49 ± 0.17	0.16 ± 0.02
	Volatile suspended solids (mg/l)	1.27 ± 0.34	0.72 ± 0.10
	Total suspended solids (mg/l)	1.76 ± 0.28	0.88 ± 0.11
	Conductivity (µS/mol)	71.14 ± 3.39	105.84 ± 3.96
	pH	7.19 ± 0.14	8.51 ± 0.41
	Temperature (° C)	16.43 ± 1.60	20.46 ± 1.20
L 6	Total nitrogen (µg/l)	597.14 ± 135.36	1216.00 ± 38.68
	Total phosphorus (µg/l)	70.71 ± 24.02	50.80 ± 3.15
	Calcium (mg/l)	3.75 ± 0.26	10.98 ± 0.39
	Sodium (mg/l)	0.62 ± 0.09	1.90 ± 1.10

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 6	Magnesium (mg/l)	2.16 ± 0.18	6.80 ± 0.26
	Potassium (mg/l)	3.16 ± 0.28	9.08 ± 0.79
	Chloride (mg/l)	0.81 ± 0.12	1.44 ± 0.19
	Sulfate (mg/l)	1.07 ± 0.21	0.00 ± 0.00
	Chlorophyll (µg/l)	5.27 ± 1.74	5.54 ± 1.58
	Non-volatile suspended solids (mg/l)	0.44 ± 0.15	0.34 ± 0.10
	Volatile suspended solids (mg/l)	1.49 ± 0.33	1.34 ± 0.17
	Total suspended solids (mg/l)	1.93 ± 0.26	1.68 ± 0.27
	Conductivity (µS/mol)	49.29 ± 3.60	127.74 ± 2.22
	pH	6.59 ± 0.11	7.02 ± 0.10
	Temperature (° C)	17.86 ± 1.16	19.36 ± 1.45
L 12	Total nitrogen (µg/l)	296.00 ± 48.23	1014.00 ± 97.09
	Total phosphorus (µg/l)	44.83 ± 12.08	84.80 ± 11.50
	Calcium (mg/l)	8.40 ± 1.72	19.42 ± 3.31
	Sodium (mg/l)	1.26 ± 0.09	4.14 ± 2.09
	Magnesium (mg/l)	4.03 ± 0.75	8.30 ± 1.33
	Potassium (mg/l)	3.45 ± 0.33	7.12 ± 0.89
	Chloride (mg/l)	0.90 ± 0.16	2.33 ± 0.25
	Sulfate (mg/l)	3.10 ± 1.28	0.00 ± 0.00
	Chlorophyll (µg/l)	4.06 ± 1.25	5.96 ± 0.66
	Non-volatile suspended solids (mg/l)	0.87 ± 0.32	1.50 ± 0.57
	Volatile suspended solids (mg/l)	2.23 ± 0.88	4.06 ± 0.83
	Total suspended solids (mg/l)	3.10 ± 1.09	5.56 ± 0.99
	Conductivity (µS/mol)	95.57 ± 17.57	181.02 ± 27.05
	pH	6.27 ± 0.11	6.60 ± 0.09
	Temperature (° C)	15.43 ± 1.19	17.12 ± 1.40
L 13	Total nitrogen (µg/l)	501.67 ± 165.72	980.00 ± 54.47
	Total phosphorus (µg/l)	19.71 ± 1.92	55.33 ± 5.02

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 13	Calcium (mg/l)	11.83 ± 0.93	20.67 ± 0.95
	Sodium (mg/l)	1.22 ± 0.05	2.55 ± 0.29
	Magnesium (mg/l)	4.79 ± 0.33	8.30 ± 0.39
	Potassium (mg/l)	2.31 ± 0.22	5.88 ± 0.44
	Chloride (mg/l)	0.70 ± 0.12	2.10 ± 0.19
	Sulfate (mg/l)	0.90 ± 0.27	0.00 ± 0.00
	Chlorophyll (µg/l)	2.36 ± 0.36	10.12 ± 4.55
	Non-volatile suspended solids (mg/l)	0.70 ± 0.27	1.37 ± 0.16
	Volatile suspended solids (mg/l)	1.00 ± 0.38	2.63 ± 0.59
	Total suspended solids (mg/l)	1.70 ± 0.38	4.00 ± 0.74
	Conductivity (µS/mol)	106.86 ± 7.49	177.32 ± 6.05
	pH	6.93 ± 0.13	7.25 ± 0.14
	Temperature (° C)	17.43 ± 1.43	17.93 ± 0.89
L 16	Total nitrogen (µg/l)	674.00 ± 265.62	1393.33 ± 48.00
	Total phosphorus (µg/l)	47.00 ± 4.67	56.17 ± 7.98
	Calcium (mg/l)	12.68 ± 1.11	39.70 ± 17.51
	Sodium (mg/l)	1.29 ± 0.17	2.95 ± 0.20
	Magnesium (mg/l)	3.99 ± 0.27	7.52 ± 0.24
	Potassium (mg/l)	0.85 ± 0.20	0.90 ± 0.23
	Chloride (mg/l)	1.26 ± 0.27	2.35 ± 0.16
	Sulfate (mg/l)	2.62 ± 0.37	2.83 ± 2.83
	Chlorophyll (µg/l)	5.16 ± 1.04	5.17 ± 2.02
	Non-volatile suspended solids (mg/l)	0.41 ± 0.21	0.68 ± 0.28
	Volatile suspended solids (mg/l)	1.11 ± 0.32	1.05 ± 0.30
	Total suspended solids (mg/l)	1.53 ± 0.25	1.73 ± 0.56
	Conductivity (µS/mol)	85.86 ± 6.50	154.43 ± 3.98
	pH	6.74 ± 0.13	7.55 ± 0.19
	Temperature (° C)	17.29 ± 1.06	18.58 ± 0.67

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 19	Total nitrogen (µg/l)	715.00 ± 262.01	936.67 ± 54.20
	Total phosphorus (µg/l)	65.14 ± 11.42	26.00 ± 1.73
	Calcium (mg/l)	4.95 ± 1.28	13.75 ± 1.98
	Sodium (mg/l)	0.90 ± 0.13	2.60 ± 0.12
	Magnesium (mg/l)	2.17 ± 0.39	5.18 ± 0.20
	Potassium (mg/l)	2.48 ± 0.22	3.10 ± 0.44
	Chloride (mg/l)	0.86 ± 0.32	1.03 ± 0.18
	Sulfate (mg/l)	1.79 ± 0.63	0.00 ± 0.00
	Chlorophyll (µg/l)	6.64 ± 2.64	1.60 ± 0.25
	Non-volatile suspended solids (mg/l)	0.33 ± 0.44	0.28 ± 0.10
	Volatile suspended solids (mg/l)	1.84 ± 0.57	0.87 ± 0.11
	Total suspended solids (mg/l)	2.17 ± 0.61	1.15 ± 0.21
	Conductivity (µS/mol)	47.71 ± 6.49	104.03 ± 5.66
	pH	6.71 ± 0.18	8.65 ± 0.43
	Temperature (° C)	16.71 ± 1.41	19.18 ± 0.91
L 21	Total nitrogen (µg/l)	498.33 ± 248.25	930.00 ± 39.33
	Total phosphorus (µg/l)	25.00 ± 5.69	26.17 ± 2.50
	Calcium (mg/l)	3.07 ± 0.64	7.48 ± 0.39
	Sodium (mg/l)	0.70 ± 0.12	1.48 ± 0.14
	Magnesium (mg/l)	1.31 ± 0.27	3.33 ± 0.19
	Potassium (mg/l)	2.30 ± 0.18	2.73 ± 0.42
	Chloride (mg/l)	0.71 ± 0.14	1.04 ± 0.16
	Sulfate (mg/l)	0.63 ± 0.17	0.00 ± 0.00
	Chlorophyll (µg/l)	4.26 ± 1.27	5.85 ± 0.73
	Non-volatile suspended solids (mg/l)	0.77 ± 0.59	0.15 ± 0.08
	Volatile suspended solids (mg/l)	0.56 ± 0.19	1.23 ± 0.11
	Total suspended solids (mg/l)	1.33 ± 0.56	1.38 ± 0.12
	Conductivity (µS/mol)	33.29 ± 4.10	70.88 ± 2.03

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 21	pH	7.01 ± 0.17	7.65 ± 0.21
	Temperature (° C)	16.14 ± 1.55	18.65 ± 1.52
L 22	Total nitrogen (µg/l)	358.57 ± 198.20	533.33 ± 44.92
	Total phosphorus (µg/l)	21.86 ± 5.89	13.33 ± 1.73
	Calcium (mg/l)	14.10 ± 0.66	10.57 ± 0.59
	Sodium (mg/l)	1.42 ± 0.09	1.35 ± 0.19
	Magnesium (mg/l)	5.77 ± 0.19	4.15 ± 0.26
	Potassium (mg/l)	1.63 ± 0.12	2.97 ± 0.25
	Chloride (mg/l)	0.56 ± 0.11	0.86 ± 0.09
	Sulfate (mg/l)	0.67 ± 0.16	0.00 ± 0.00
	Chlorophyll (µg/l)	1.31 ± 0.21	1.13 ± 0.11
	Non-volatile suspended solids (mg/l)	0.24 ± 0.18	0.07 ± 0.05
	Volatile suspended solids (mg/l)	0.14 ± 0.07	0.62 ± 0.11
	Total suspended solids (mg/l)	0.39 ± 0.17	0.68 ± 0.15
	Conductivity (µS/mol)	121.14 ± 4.48	93.15 ± 4.18
	pH	7.59 ± 0.09	7.56 ± 0.13
	Temperature (° C)	17.43 ± 1.51	19.05 ± 1.11
L 23	Total nitrogen (µg/l)	602.86 ± 192.46	1240.00 ± 39.67
	Total phosphorus (µg/l)	52.57 ± 11.46	36.00 ± 2.98
	Calcium (mg/l)	6.21 ± 0.47	9.23 ± 0.18
	Sodium (mg/l)	1.15 ± 0.09	1.78 ± 0.21
	Magnesium (mg/l)	3.07 ± 0.17	4.65 ± 0.19
	Potassium (mg/l)	3.53 ± 0.18	5.57 ± 0.18
	Chloride (mg/l)	1.26 ± 0.40	1.62 ± 0.08
	Sulfate (mg/l)	1.77 ± 0.58	0.00 ± 0.00
	Chlorophyll (µg/l)	5.44 ± 2.96	3.82 ± 0.45
	Non-volatile suspended solids (mg/l)	0.24 ± 0.08	0.15 ± 0.07
	Volatile suspended solids (mg/l)	0.56 ± 0.19	0.92 ± 0.09

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 23	Total suspended solids (mg/l)	0.80 ± 0.18	1.07 ± 0.10
	Conductivity (µS/mol)	62.00 ± 3.24	98.08 ± 1.25
	pH	6.76 ± 0.22	7.58 ± 0.13
	Temperature (° C)	17.43 ± 1.84	20.10 ± 1.02
L 24	Total nitrogen (µg/l)	238.00 ± 110.61	283.33 ± 29.06
	Total phosphorus (µg/l)	31.43 ± 14.12	5.50 ± 1.06
	Calcium (mg/l)	17.14 ± 1.67	26.52 ± 1.76
	Sodium (mg/l)	2.87 ± 0.17	3.23 ± 0.36
	Magnesium (mg/l)	9.72 ± 1.06	13.48 ± 1.21
	Potassium (mg/l)	4.19 ± 0.15	5.95 ± 0.33
	Chloride (mg/l)	0.93 ± 0.14	1.68 ± 0.10
	Sulfate (mg/l)	0.41 ± 0.09	0.00 ± 0.00
	Chlorophyll (µg/l)	0.53 ± 0.11	0.37 ± 0.03
	Non-volatile suspended solids (mg/l)	0.07 ± 0.07	0.03 ± 0.03
	Volatile suspended solids (mg/l)	0.16 ± 0.09	0.25 ± 0.04
	Total suspended solids (mg/l)	0.23 ± 0.07	0.28 ± 0.03
	Conductivity (µS/mol)	205.14 ± 14.42	248.03 ± 16.70
	pH	8.00 ± 0.00	8.41 ± 0.10
	Temperature (° C)	18.57 ± 1.59	20.07 ± 1.16
L 26	Total nitrogen (µg/l)	637.14 ± 170.83	1030.00 ± 40.41
	Total phosphorus (µg/l)	37.00 ± 6.53	31.45 ± 2.39
	Calcium (mg/l)	12.80 ± 0.96	20.35 ± 0.24
	Sodium (mg/l)	1.91 ± 0.11	3.24 ± 0.17
	Magnesium (mg/l)	5.40 ± 0.43	8.58 ± 0.12
	Potassium (mg/l)	1.91 ± 0.24	2.15 ± 0.38
	Chloride (mg/l)	0.87 ± 0.15	1.44 ± 0.14
	Sulfate (mg/l)	1.42 ± 0.37	0.00 ± 0.00
	Chlorophyll (µg/l)	3.09 ± 0.47	2.91 ± 0.55

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 26	Non-volatile suspended solids (mg/l)	0.26 ± 0.07	0.24 ± 0.03
	Volatile suspended solids (mg/l)	0.77 ± 0.21	0.86 ± 0.09
	Total suspended solids (mg/l)	1.03 ± 0.22	1.10 ± 0.10
	Conductivity (µS/mol)	120.43 ± 8.19	162.43 ± 1.52
	pH	7.49 ± 0.17	8.00 ± 0.23
	Temperature (° C)	18.17 ± 1.22	18.94 ± 0.79
L 27	Total nitrogen (µg/l)	498.00 ± 89.07	1308.33 ± 53.00
	Total phosphorus (µg/l)	52.33 ± 6.26	94.17 ± 17.48
	Calcium (mg/l)	11.18 ± 0.85	17.78 ± 0.49
	Sodium (mg/l)	1.33 ± 0.11	3.08 ± 0.16
	Magnesium (mg/l)	3.90 ± 0.14	6.73 ± 0.21
	Potassium (mg/l)	1.25 ± 0.22	2.17 ± 0.46
	Chloride (mg/l)	0.99 ± 0.20	1.93 ± 0.25
	Sulfate (mg/l)	1.78 ± 0.31	0.00 ± 0.00
	Chlorophyll (µg/l)	4.19 ± 0.81	5.77 ± 1.69
	Non-volatile suspended solids (mg/l)	0.17 ± 0.10	0.35 ± 0.12
	Volatile suspended solids (mg/l)	0.84 ± 0.24	1.10 ± 0.18
	Total suspended solids (mg/l)	1.01 ± 0.20	1.45 ± 0.21
	Conductivity (µS/mol)	89.00 ± 5.79	134.93 ± 2.63
	pH	7.07 ± 0.13	8.05 ± 0.50
	Temperature (° C)	18.57 ± 1.49	19.42 ± 1.23
L 28	Total nitrogen (µg/l)	385.00 ± 187.19	535.00 ± 52.33
	Total phosphorus (µg/l)	24.57 ± 11.77	8.83 ± 0.70
	Calcium (mg/l)	19.53 ± 1.96	23.15 ± 2.00
	Sodium (mg/l)	2.02 ± 0.07	2.67 ± 0.26
	Magnesium (mg/l)	8.88 ± 0.20	10.03 ± 0.95
	Potassium (mg/l)	3.77 ± 0.10	5.15 ± 0.41
	Chloride (mg/l)	0.76 ± 0.12	1.46 ± 0.06

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 28	Sulfate (mg/l)	1.09 ± 0.51	0.00 ± 0.00
	Chlorophyll (µg/l)	2.47 ± 1.73	0.88 ± 0.17
	Non-volatile suspended solids (mg/l)	0.21 ± 0.12	0.03 ± 0.02
	Volatile suspended solids (mg/l)	0.21 ± 0.07	0.43 ± 0.06
	Total suspended solids (mg/l)	0.43 ± 0.11	0.47 ± 0.07
	Conductivity (µS/mol)	180.14 ± 5.22	199.08 ± 17.30
	pH	8.00 ± 0.00	8.08 ± 0.12
	Temperature (° C)	18.86 ± 1.67	19.07 ± 0.98
L 29	Total nitrogen (µg/l)	576.00 ± 186.70	1021.67 ± 68.38
	Total phosphorus (µg/l)	26.57 ± 5.79	40.33 ± 3.73
	Calcium (mg/l)	8.40 ± 0.62	8.02 ± 0.65
	Sodium (mg/l)	1.88 ± 0.12	1.85 ± 0.30
	Magnesium (mg/l)	3.96 ± 0.28	2.93 ± 0.25
	Potassium (mg/l)	1.95 ± 0.12	3.87 ± 0.42
	Chloride (mg/l)	1.01 ± 0.25	1.21 ± 0.17
	Sulfate (mg/l)	1.17 ± 0.21	0.00 ± 0.00
	Chlorophyll (µg/l)	2.79 ± 0.68	8.80 ± 1.70
	Non-volatile suspended solids (mg/l)	0.64 ± 0.53	0.28 ± 0.11
	Volatile suspended solids (mg/l)	0.80 ± 0.27	2.02 ± 0.40
	Total suspended solids (mg/l)	1.44 ± 0.55	2.30 ± 0.38
	Conductivity (µS/mol)	82.14 ± 4.17	73.50 ± 4.18
	pH	6.94 ± 0.17	6.83 ± 0.08
	Temperature (° C)	17.43 ± 1.36	18.27 ± 0.65
L 30	Total nitrogen (µg/l)	585.00 ± 216.68	1273.33 ± 108.80
	Total phosphorus (µg/l)	25.71 ± 4.42	28.83 ± 2.81
	Calcium (mg/l)	8.37 ± 0.69	8.78 ± 0.46
	Sodium (mg/l)	1.53 ± 0.11	1.92 ± 0.27
	Magnesium (mg/l)	3.76 ± 0.16	3.73 ± 0.20

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 30	Potassium (mg/l)	1.93 ± 0.14	4.63 ± 0.73
	Chloride (mg/l)	1.01 ± 0.22	2.22 ± 0.28
	Sulfate (mg/l)	1.27 ± 0.28	0.00 ± 0.00
	Chlorophyll (µg/l)	2.03 ± 0.41	7.05 ± 2.57
	Non-volatile suspended solids (mg/l)	0.03 ± 0.16	0.33 ± 0.10
	Volatile suspended solids (mg/l)	0.71 ± 0.23	1.93 ± 0.55
	Total suspended solids (mg/l)	0.74 ± 0.17	2.27 ± 0.63
	Conductivity (µS/mol)	71.57 ± 5.04	88.58 ± 4.88
	pH	6.76 ± 0.13	6.82 ± 0.06
	Temperature (° C)	18.29 ± 0.94	17.07 ± 0.83
L 31	Total nitrogen (µg/l)	412.00 ± 66.89	1676.67 ± 87.09
	Total phosphorus (µg/l)	32.86 ± 3.49	92.83 ± 16.36
	Calcium (mg/l)	12.29 ± 0.63	25.95 ± 3.00
	Sodium (mg/l)	1.29 ± 0.07	2.97 ± 0.43
	Magnesium (mg/l)	4.24 ± 0.14	9.32 ± 1.32
	Potassium (mg/l)	0.74 ± 0.21	1.52 ± 0.68
	Chloride (mg/l)	1.51 ± 0.30	2.39 ± 0.53
	Sulfate (mg/l)	2.87 ± 0.71	0.00 ± 0.00
	Chlorophyll (µg/l)	3.06 ± 0.48	3.85 ± 0.86
	Non-volatile suspended solids (mg/l)	0.24 ± 0.13	1.22 ± 0.34
	Volatile suspended solids (mg/l)	0.61 ± 0.20	1.08 ± 0.19
	Total suspended solids (mg/l)	0.86 ± 0.13	2.30 ± 0.44
	Conductivity (µS/mol)	90.43 ± 5.34	180.68 ± 24.19
	pH	7.19 ± 0.09	7.95 ± 0.50
	Temperature (° C)	18.29 ± 1.11	17.18 ± 0.74
L 60	Total nitrogen (µg/l)	384.00 ± 37.50	1465.45 ± 62.27
	Total phosphorus (µg/l)	53.00 ± 4.63	67.91 ± 7.37
	Calcium (mg/l)	10.67 ± 1.02	18.00 ± 0.59

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
L 60	Sodium (mg/l)	1.37 ± 0.13	3.37 ± 0.26
	Magnesium (mg/l)	3.81 ± 0.20	7.12 ± 0.20
	Potassium (mg/l)	1.91 ± 0.24	2.96 ± 0.43
	Chloride (mg/l)	1.00 ± 0.20	1.90 ± 0.21
	Sulfate (mg/l)	1.36 ± 0.29	0.00 ± 0.00
	Chlorophyll (µg/l)	3.57 ± 0.68	5.33 ± 0.78
	Non-volatile suspended solids (mg/l)	0.61 ± 0.39	0.43 ± 0.09
	Volatile suspended solids (mg/l)	1.10 ± 0.31	1.42 ± 0.12
	Total suspended solids (mg/l)	1.71 ± 0.53	1.85 ± 0.12
	Conductivity (µS/mol)	82.57 ± 5.52	143.65 ± 4.76
	pH	7.40 ± 0.16	8.94 ± 0.43
	Temperature (° C)	18.14 ± 1.16	19.03 ± 1.07
M 20	Total nitrogen (µg/l)	3536.25 ± 599.31	9770.91 ± 412.91
	Total phosphorus (µg/l)	1687.00 ± 123.18	2610.73 ± 180.19
	Calcium (mg/l)	32.04 ± 2.76	34.89 ± 3.34
	Sodium (mg/l)	106.76 ± 14.76	194.18 ± 5.59
	Magnesium (mg/l)	122.72 ± 9.63	181.30 ± 4.17
	Potassium (mg/l)	49.67 ± 13.82	38.85 ± 1.04
	Chloride (mg/l)	11.95 ± 3.47	67.53 ± 1.36
	Sulfate (mg/l)	4.19 ± 0.41	0.00 ± 0.00
	Chlorophyll (µg/l)	60.73 ± 17.37	6.93 ± 1.75
	Non-volatile suspended solids (mg/l)	3.91 ± 1.85	1.38 ± 0.17
	Volatile suspended solids (mg/l)	15.60 ± 5.14	4.20 ± 0.61
	Total suspended solids (mg/l)	19.51 ± 4.96	5.58 ± 0.59
	Conductivity (µS/mol)	1410.63 ± 84.85	1659.64 ± 39.29
	pH	9.56 ± 0.26	9.38 ± 0.09
	Temperature (° C)	18.50 ± 1.48	18.84 ± 0.67
M 22	Total nitrogen (µg/l)	1190.00 ± 290.52	6752.50 ± 647.33

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
M 22	Total phosphorus (µg/l)	2079.71 ± 272.44	5032.75 ± 518.04
	Calcium (mg/l)	32.26 ± 1.89	34.68 ± 1.89
	Sodium (mg/l)	73.59 ± 7.45	81.80 ± 13.31
	Magnesium (mg/l)	48.56 ± 6.78	56.50 ± 3.26
	Potassium (mg/l)	26.05 ± 1.79	42.20 ± 1.63
	Chloride (mg/l)	9.46 ± 3.49	46.44 ± 6.68
	Sulfate (mg/l)	8.49 ± 3.99	2.25 ± 1.93
	Chlorophyll (µg/l)	4.37 ± 0.78	10.23 ± 2.54
	Non-volatile suspended solids (mg/l)	1.01 ± 0.56	1.98 ± 0.36
	Volatile suspended solids (mg/l)	2.10 ± 0.60	6.93 ± 1.07
	Total suspended solids (mg/l)	3.11 ± 1.11	8.90 ± 1.33
	Conductivity (µS/mol)	932.29 ± 119.36	889.00 ± 57.46
	pH	8.37 ± 0.31	7.52 ± 0.16
	Temperature (° C)	14.57 ± 1.56	16.95 ± 1.91
M 24	Total nitrogen (µg/l)	965.71 ± 212.41	7737.50 ± 1935.46
	Total phosphorus (µg/l)	442.29 ± 83.91	4728.75 ± 2450.87
	Calcium (mg/l)	11.15 ± 1.86	14.48 ± 2.12
	Sodium (mg/l)	4.49 ± 0.34	2.20 ± 0.81
	Magnesium (mg/l)	5.04 ± 0.95	6.35 ± 0.76
	Potassium (mg/l)	8.95 ± 1.00	33.38 ± 9.60
	Chloride (mg/l)	1.73 ± 0.18	5.81 ± 2.50
	Sulfate (mg/l)	1.66 ± 0.35	560.25 ± 550.28
	Chlorophyll (µg/l)	22.67 ± 9.03	253.95 ± 179.74
	Non-volatile suspended solids (mg/l)	5.34 ± 2.50	7.55 ± 4.41
	Volatile suspended solids (mg/l)	6.40 ± 2.29	32.75 ± 20.93
	Total suspended solids (mg/l)	11.74 ± 4.62	40.30 ± 25.30
	Conductivity (µS/mol)	140.00 ± 11.06	218.15 ± 45.38
	pH	6.89 ± 0.52	6.82 ± 0.13

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
M 24	Temperature (° C)	14.00 ± 1.29	15.65 ± 1.88
M 25	Total nitrogen (µg/l)	2126.67 ± 541.82	18439.09 ± 1542.58
	Total phosphorus (µg/l)	379.86 ± 34.76	1044.27 ± 164.71
	Calcium (mg/l)	36.75 ± 4.90	51.37 ± 3.70
	Sodium (mg/l)	66.27 ± 4.53	332.15 ± 14.62
	Magnesium (mg/l)	49.61 ± 4.31	185.09 ± 3.55
	Potassium (mg/l)	25.39 ± 1.16	104.22 ± 4.60
	Chloride (mg/l)	9.11 ± 2.20	160.97 ± 6.03
	Sulfate (mg/l)	3.18 ± 0.26	463.18 ± 27.17
	Chlorophyll (µg/l)	11.83 ± 7.55	7.65 ± 1.86
	Non-volatile suspended solids (mg/l)	1.17 ± 0.57	2.30 ± 0.37
	Volatile suspended solids (mg/l)	2.96 ± 1.92	4.92 ± 0.56
	Total suspended solids (mg/l)	4.13 ± 2.28	7.22 ± 0.86
	Conductivity (µS/mol)	791.71 ± 28.18	2540.00 ± 73.25
	pH	9.40 ± 0.28	8.99 ± 0.14
	Temperature (° C)	16.43 ± 1.41	20.29 ± 0.98
M 27	Total nitrogen (µg/l)	1358.00 ± 269.23	5523.33 ± 536.39
	Total phosphorus (µg/l)	901.86 ± 298.48	3690.83 ± 507.73
	Calcium (mg/l)	45.86 ± 5.48	127.68 ± 16.62
	Sodium (mg/l)	17.58 ± 3.84	19.77 ± 2.25
	Magnesium (mg/l)	26.30 ± 0.55	56.78 ± 7.22
	Potassium (mg/l)	12.21 ± 0.74	48.55 ± 5.78
	Chloride (mg/l)	4.16 ± 0.87	24.68 ± 2.47
	Sulfate (mg/l)	2.86 ± 0.71	171.50 ± 67.68
	Chlorophyll (µg/l)	12.73 ± 5.26	21.67 ± 8.95
	Non-volatile suspended solids (mg/l)	2.86 ± 0.74	6.63 ± 3.25
	Volatile suspended solids (mg/l)	3.64 ± 1.07	12.68 ± 4.70
	Total suspended solids (mg/l)	6.50 ± 1.61	19.32 ± 7.91

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
M 27	Conductivity (µS/mol)	458.43 ± 22.70	1059.17 ± 107.49
	pH	7.77 ± 0.10	7.40 ± 0.17
	Temperature (° C)	16.00 ± 1.69	17.40 ± 1.40
M 28	Total nitrogen (µg/l)	1415.00 ± 105.24	4141.67 ± 305.88
	Total phosphorus (µg/l)	189.29 ± 49.19	184.83 ± 31.00
	Calcium (mg/l)	26.81 ± 3.04	34.62 ± 2.30
	Sodium (mg/l)	11.85 ± 0.61	24.22 ± 1.25
	Magnesium (mg/l)	23.31 ± 0.45	41.07 ± 1.76
	Potassium (mg/l)	10.31 ± 0.36	18.17 ± 0.25
	Chloride (mg/l)	2.94 ± 0.46	12.46 ± 0.89
	Sulfate (mg/l)	2.87 ± 0.38	92.83 ± 6.74
	Chlorophyll (µg/l)	43.93 ± 7.36	8.63 ± 2.21
	Non-volatile suspended solids (mg/l)	3.20 ± 0.99	0.45 ± 0.11
	Volatile suspended solids (mg/l)	8.40 ± 3.21	2.60 ± 0.59
	Total suspended solids (mg/l)	11.60 ± 2.81	3.05 ± 0.54
	Conductivity (µS/mol)	334.29 ± 9.35	527.17 ± 18.88
	pH	9.29 ± 0.21	9.82 ± 0.22
	Temperature (° C)	18.60 ± 1.91	19.58 ± 1.57
M 37	Total nitrogen (µg/l)	1834.00 ± 218.92	3778.33 ± 327.77
	Total phosphorus (µg/l)	215.29 ± 36.51	528.17 ± 161.91
	Calcium (mg/l)	28.56 ± 2.09	160.80 ± 13.64
	Sodium (mg/l)	18.46 ± 2.24	7.50 ± 0.77
	Magnesium (mg/l)	26.01 ± 1.55	44.24 ± 5.57
	Potassium (mg/l)	25.72 ± 1.73	59.13 ± 7.66
	Chloride (mg/l)	7.51 ± 0.43	23.78 ± 3.99
	Sulfate (mg/l)	4.81 ± 1.18	273.17 ± 38.14
	Chlorophyll (µg/l)	23.74 ± 6.44	30.65 ± 13.66
	Non-volatile suspended solids (mg/l)	1.59 ± 0.71	1.48 ± 0.54

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
M 37	Volatile suspended solids (mg/l)	4.41 ± 2.05	4.92 ± 0.90
	Total suspended solids (mg/l)	6.00 ± 2.22	6.40 ± 1.37
	Conductivity (µS/mol)	444.43 ± 23.25	1138.00 ± 87.63
	pH	9.36 ± 0.26	7.42 ± 0.05
	Temperature (° C)	16.71 ± 1.25	17.27 ± 0.83
M 49	Total nitrogen (µg/l)	808.33 ± 183.73	3945.00 ± 260.84
	Total phosphorus (µg/l)	138.29 ± 23.50	2013.33 ± 221.55
	Calcium (mg/l)	29.97 ± 2.89	74.05 ± 6.40
	Sodium (mg/l)	15.47 ± 1.72	13.28 ± 0.79
	Magnesium (mg/l)	24.64 ± 1.19	39.02 ± 3.34
	Potassium (mg/l)	12.04 ± 1.53	28.57 ± 4.10
	Chloride (mg/l)	3.50 ± 0.70	15.21 ± 1.80
	Sulfate (mg/l)	2.40 ± 0.50	168.00 ± 35.14
	Chlorophyll (µg/l)	14.59 ± 5.20	32.10 ± 11.01
	Non-volatile suspended solids (mg/l)	0.64 ± 0.27	3.03 ± 0.73
	Volatile suspended solids (mg/l)	1.66 ± 0.64	7.98 ± 1.46
	Total suspended solids (mg/l)	2.30 ± 0.60	11.02 ± 1.94
	Conductivity (µS/mol)	402.57 ± 26.35	712.83 ± 53.02
	pH	8.51 ± 0.36	7.00 ± 0.12
	Temperature (° C)	17.00 ± 1.70	14.27 ± 1.32
M 51	Total nitrogen (µg/l)	958.57 ± 178.33	5516.00 ± 529.14
	Total phosphorus (µg/l)	443.50 ± 74.68	1702.60 ± 418.70
	Calcium (mg/l)	43.57 ± 5.01	128.84 ± 19.00
	Sodium (mg/l)	18.71 ± 2.25	29.94 ± 3.24
	Magnesium (mg/l)	29.94 ± 3.41	65.12 ± 5.64
	Potassium (mg/l)	12.52 ± 1.72	36.26 ± 4.72
	Chloride (mg/l)	3.26 ± 0.77	23.57 ± 2.89
	Sulfate (mg/l)	2.10 ± 0.30	247.40 ± 123.48

Appendix A (continued)

Lake	Limnological characteristic	1985–1989	2010–2012
M 51	Chlorophyll (µg/l)	10.19 ± 3.26	10.92 ± 2.68
	Non-volatile suspended solids (mg/l)	2.79 ± 0.63	7.20 ± 2.61
	Volatile suspended solids (mg/l)	3.71 ± 0.86	11.16 ± 5.87
	Total suspended solids (mg/l)	6.50 ± 1.36	18.36 ± 8.29
	Conductivity (µS/mol)	548.14 ± 54.25	1136.00 ± 135.41
	pH	8.27 ± 0.47	7.59 ± 0.05
	Temperature (° C)	14.71 ± 1.32	16.96 ± 1.18

Appendix B. Maps of my study plots in the Yukon Flats, Alaska, showing the location and numerical code of each study lake.

Figure B-1. Map of study plot C. Inset map shows the plot location within the Yukon Flats National Wildlife Refuge boundary.

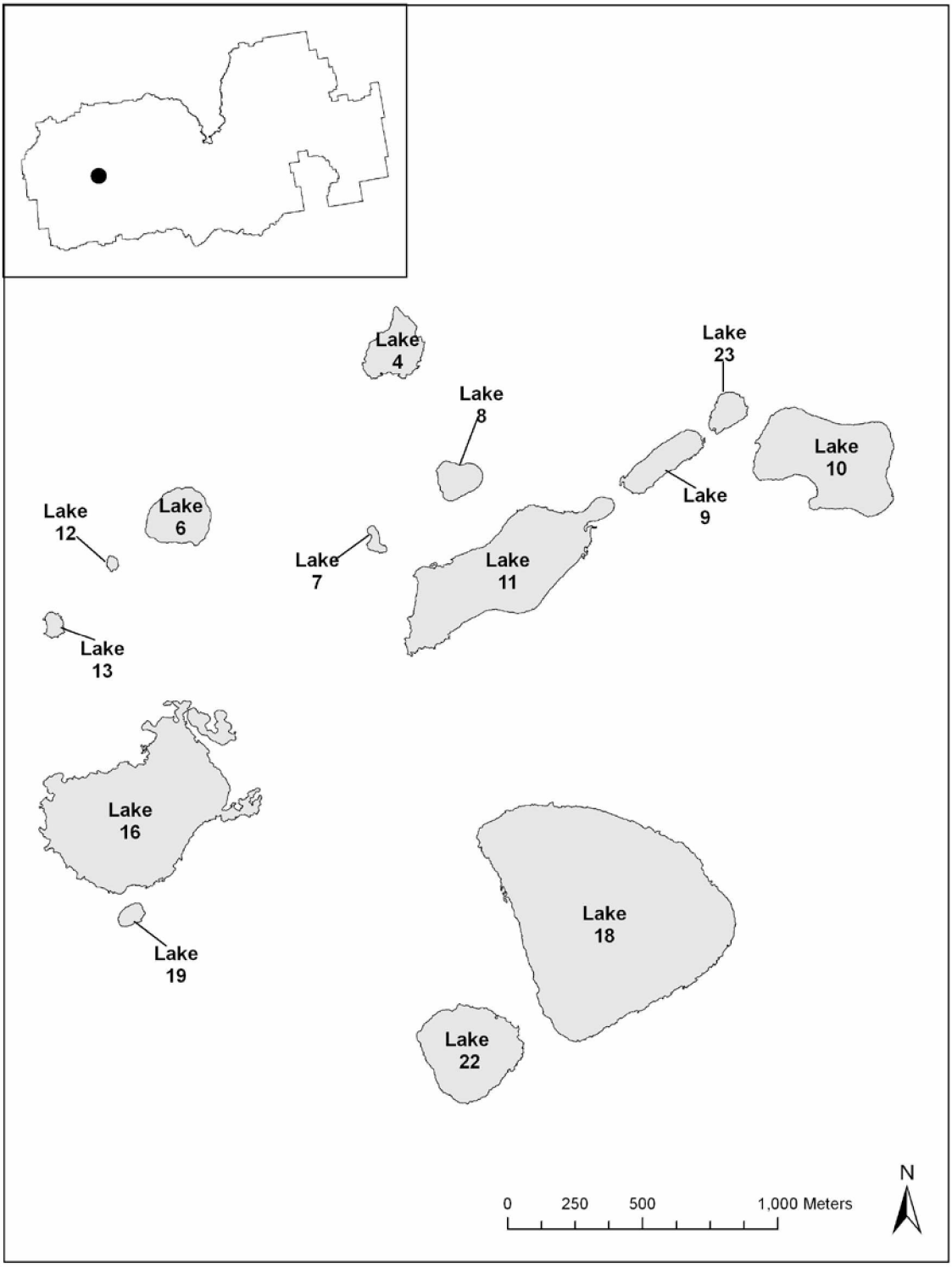

Figure B-2. Map of study plot D. Inset map shows the plot location within the Yukon Flats National Wildlife Refuge boundary.

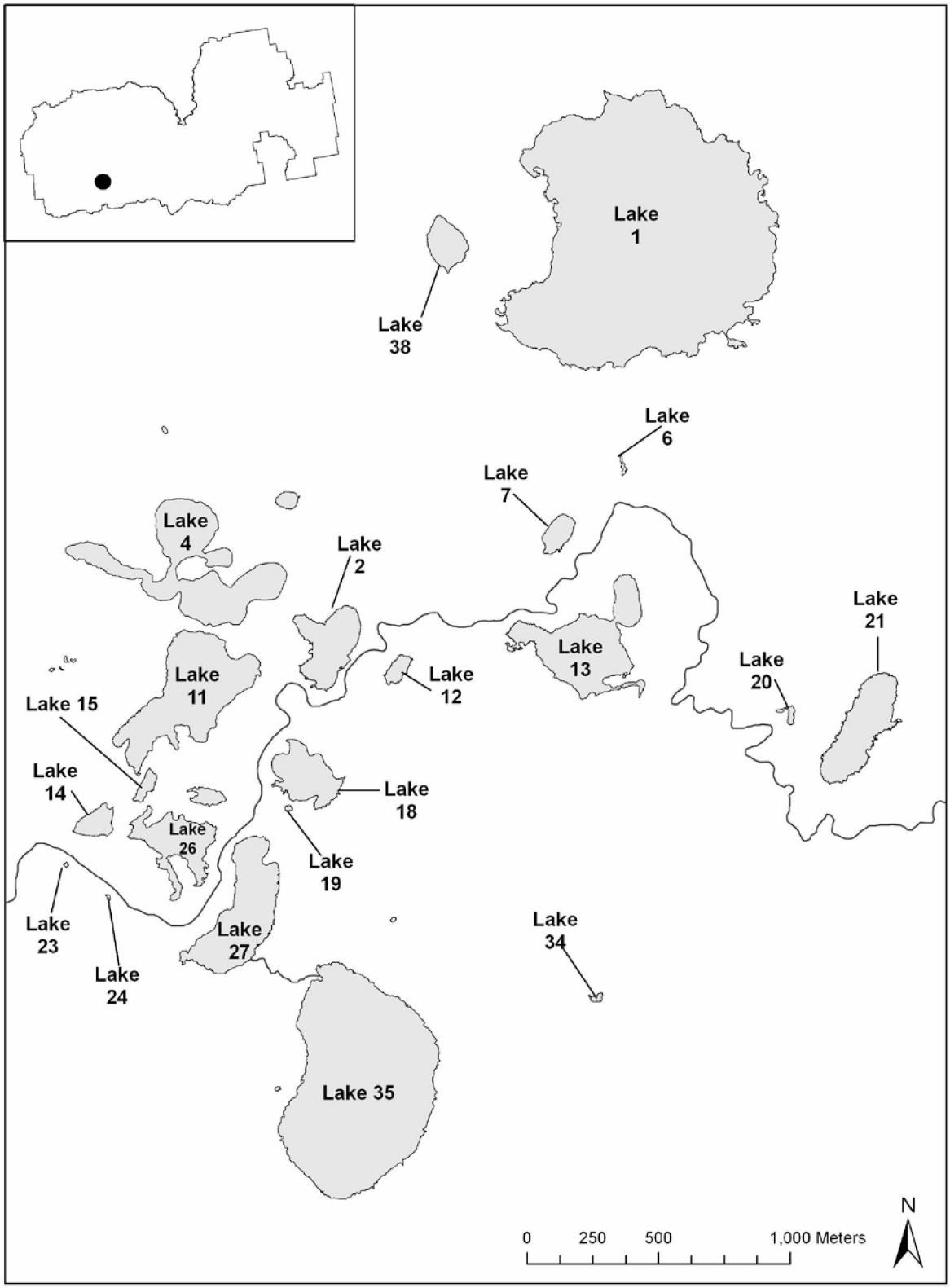

Figure B-3. Map of study plot F. Inset map shows the plot location within the Yukon Flats National Wildlife Refuge boundary.

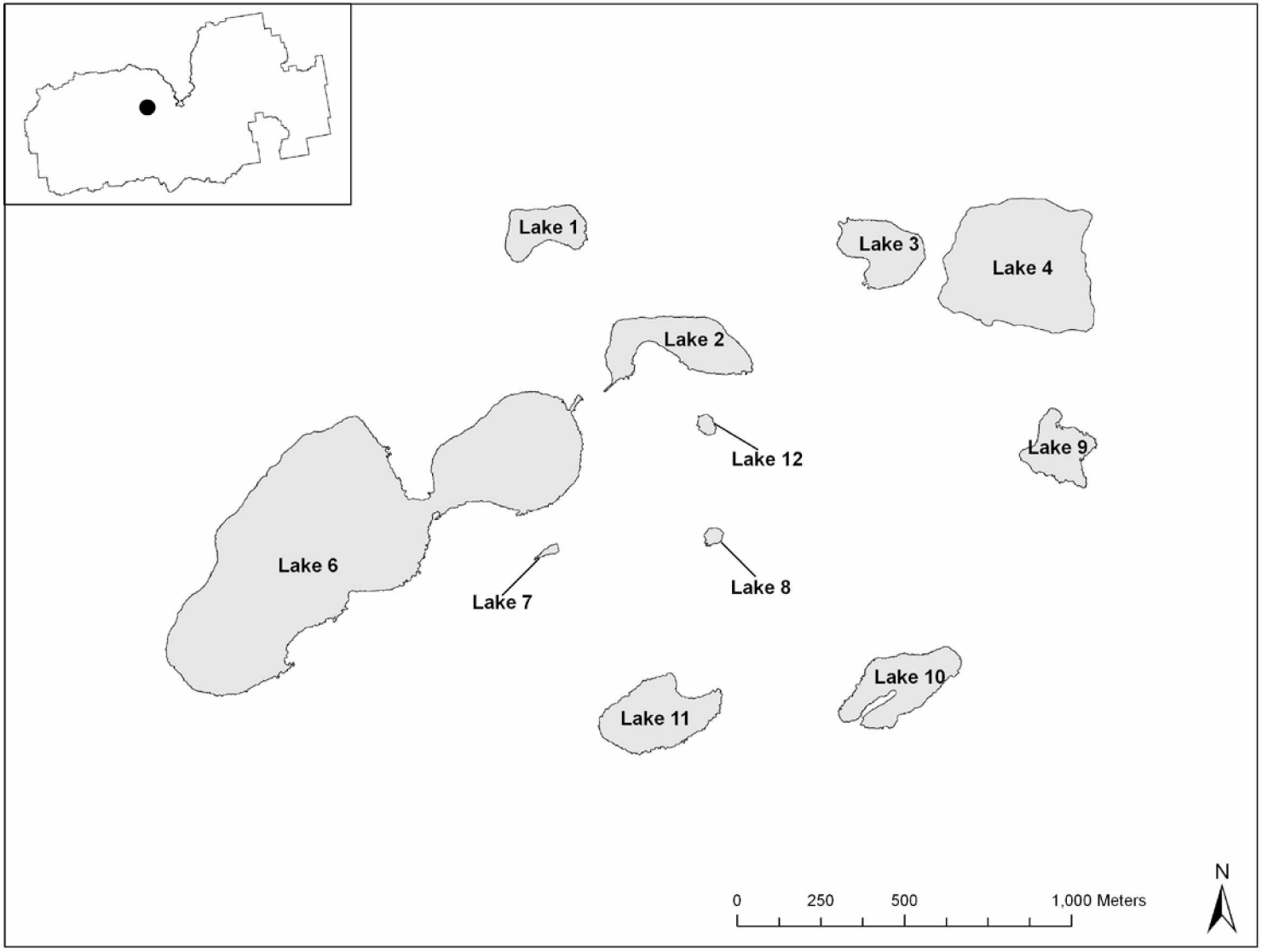

Figure B-4. Map of study plot H. Inset map shows the plot location within the Yukon Flats National Wildlife Refuge boundary.

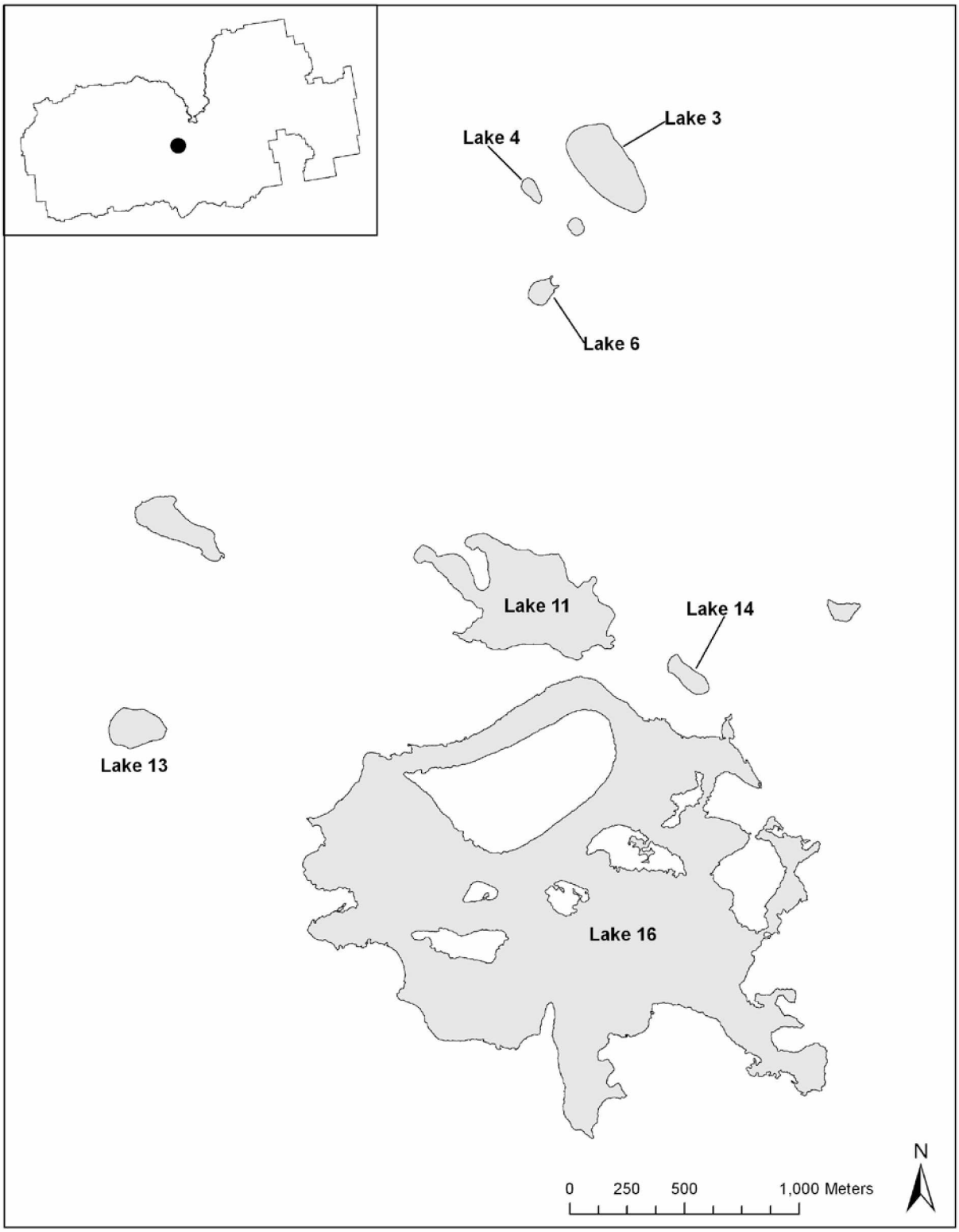

Figure B-5. Map of study plot L. Inset map shows the plot location within the Yukon Flats National Wildlife Refuge boundary.

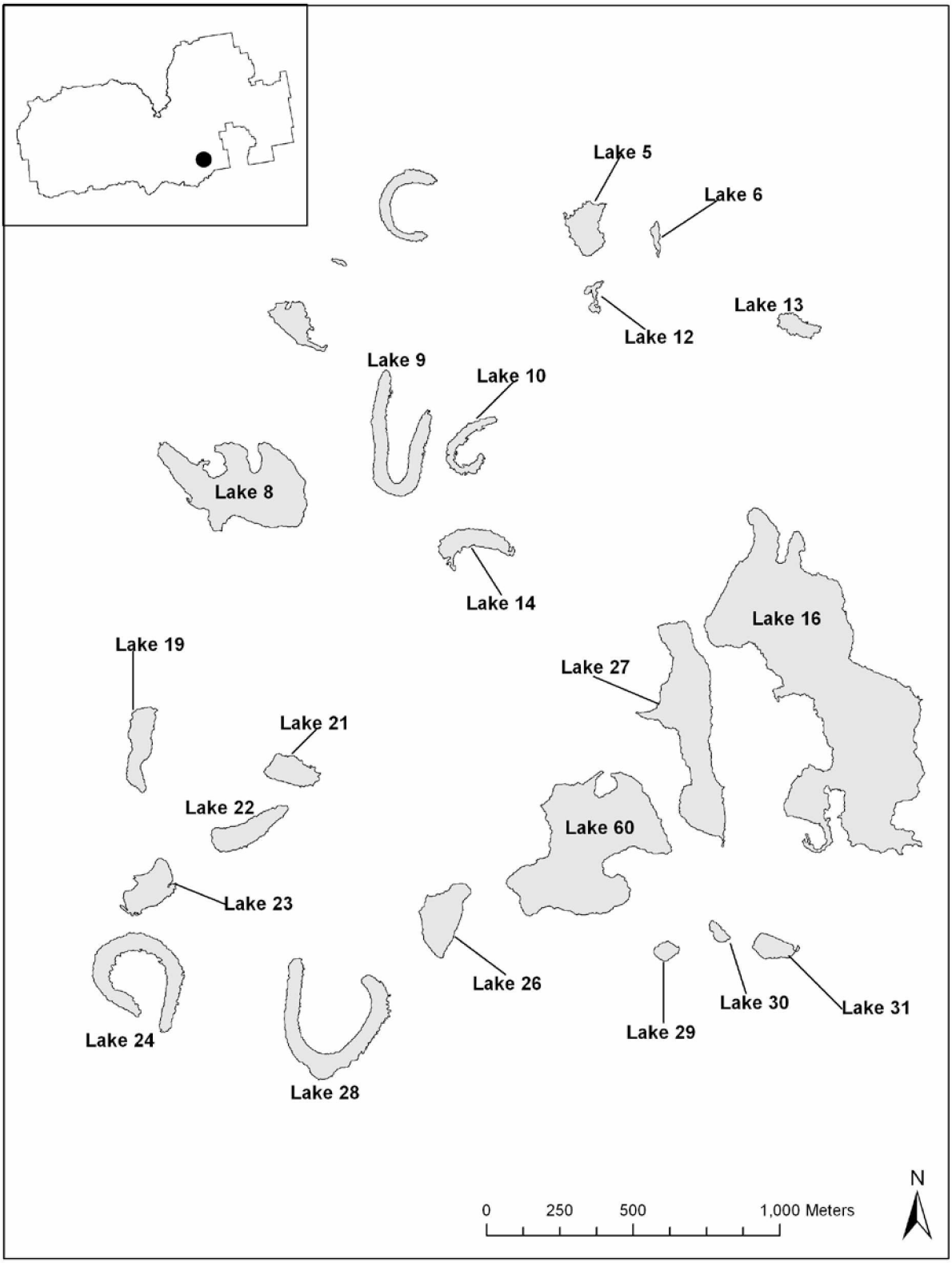

Figure B-6. Map of study plot M. Inset map shows the plot location within the Yukon Flats National Wildlife Refuge boundary.